

TEMPORARY HYDROLOGIC CONNECTIONS MAKE

“ISOLATED” WETLANDS

FUNCTION AT THE LANDSCAPE SCALE

by

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ABSTRACT

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Temporary hydrologic connections make “isolated” wetlands function at the landscape scale

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The importance of landscape-level connectivity to depressional wetland structure function is ambiguous. The ambiguity is a result of the relative significance researchers have placed on surface versus groundwater hydrology. Depressional wetlands are often characterized by small, closed basins without a naturally integrated surface drainage system. Water inputs are dominated by surface runoff. In contrast, variation in vegetation structure is often attributed to differences in wetland permanence, and salinity, both of which are reportedly driven by deep (>4 m) groundwater connections among wetlands. In opposition to both views, I compared differences in depressional wetland structure and function between wetlands with and without a temporary (<4 wk) surface water or near-surface water (<1 m) connection to an adjacent up-gradient wetland. “Connected” wetlands had greater mean wetland/catchment ratios, but stored more water, stored water longer, had higher specific conductance, and were more productive than “isolated” wetlands. Wetland plant composition of “connected wetlands” was different than that of “isolated” wetlands. I compared local hydrology, water chemistry, and soil development between groundwater discharge and non-discharge locations within wetlands and found no evidence of groundwater inputs. My results provide evidence that depressional wetland hydrology and vegetation structure are primarily determined by surface and near-surface hydrologic processes that are expressed at both the landscape and localized spatial scales. Conservation policies should incorporate depressional wetland dependence on landscape-level hydrologic processes, specifically their commonly ignored surface and near-surface hydrologic connections.

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CHAPTER I

The role of landscape-level connectivity on depressional wetland structure and function

INTRODUCTION

Wetlands are transitional ecotones between aquatic and terrestrial ecosystems (Naiman and Decamps 1990) and therefore wetland structure and function should be intimately tied to landscape processes. Landscape connectivity may profoundly affect the variation in the source, timing, duration, quantity, and quality of water input and output. However, wetlands are classic examples of ecosystems that have historically been treated as discrete units for ecological analyses and delineated as discrete units for management purposes (Bedford and Preston 1988).

Depressional wetlands are considered to be the simplest wetland type. Compared to other wetland systems, depressional wetlands have less complex geomorphic settings, water sources, and water regimes (Brinson 1993, Smith et al. 1995). Water inputs have been shown to be dominated by surface runoff from precipitation and spring snowmelt and water outputs dominated by evapotranspiration (Winter et al. 1984, Winter and Woo 1990, Mitsch and Gosselink 1993, Bedford 1996, LaBaugh et al. 1998, Hayashi et al. 1998). Examples of depressional wetlands include the vernal pools of California, the Carolina Bays of the Atlantic coastal plain, and the prairie potholes of the glaciated Northern Great Plains of Central North America. Prairie potholes, also called sloughs and kettle lakes, are the most thoroughly studied of the depressional wetland types (see Great Plains Research Vol. 8, No. 1, 1998 for a recent comprehensive review). However,

despite the apparent hydrologic and geomorphic simplicity of depressional wetlands, the importance of landscape-level connectivity to the function of these wetlands remains ambiguous in the literature.

The ambiguity of landscape-level connectivity within and between depressional wetland structure and function is a result of the relative significance researchers have placed on surface versus groundwater hydrology. Many researchers have characterized depressional wetlands as small, closed basins without a naturally integrated surface drainage system (Winter and Woo 1990, Brinson 1993, Mitsch and Gosselink 1993, Bedford 1996, Hayashi et al. 1998). Surface water connections between depressional wetlands appear to be rare, restricted to very brief periods during high water storage, and have little effect on overall wetland hydrology. The apparent lack of surface water connections has lead both scientists and wetland managers to treat depressional wetlands as independently functioning, discrete units on the landscape (Bedford and Preston 1988).

A good example of how both scientists and managers have treated wetlands, and especially depressional wetlands, is the legal protection given to wetlands by the U.S. Federal Government. Section 404 of the Clean Water Act (CWA, formerly the Federal Water Pollution Control Act, 33 U.S.C. 1344) is the primary vehicle for wetland protection in the U.S. Through the CWA, wetlands are the only land-type to be comprehensively regulated across both public and private lands within the United States (National Research Council 1995). The purpose of the CWA was to "...restore and maintain the chemical, physical, and biological integrity of the waters of the United States." Provisions of the CWA include wetland protection from dredging and filling (Section 404, administered by the US Army Corps of Engineers), and protection of water

quality (e.g., Sections 301(b), 303, 401, administered by the US Environmental Protection Agency). Accompanying these regulations is a legal definition of a wetland (42 *Fed. Reg.* 37128), and a procedure to delineate wetland boundaries (Environmental Laboratory 1987). Projects come under review for protection by Section 404 only when proposed project alterations occur within the delineated wetland (see Fretwell et al. 1996, for review). Section 404 is the only Federal Regulation that affords direct protection to wetlands (Fretwell 1996). Ironically, the delineation approach to wetland protection treats wetlands as independently functioning, discrete units and implies that wetlands have no dependency on landscape-scale connectivity.

In contrast to the concept of treating depressional wetlands as discrete units on the landscape, some researchers have focused on depressional wetlands as being connected via deep groundwater. Studies with a groundwater-connectivity perspective have developed a conceptual model that uses elevation and surface water salinity as indicators of deep hydrologic connections among wetlands (Rozkowski 1967, Miller 1969, Lissey 1971, Sloan 1972, LaBaugh et al. 1987, Arndt and Richardson 1989, Richardson et al. 1992, Winter and Rosenberry 1995, LaBaugh et al. 1998). The groundwater-connectivity model contends that the balance of groundwater discharge (inputs to the wetland) and groundwater recharge (outputs from the wetland), and the movement of total dissolved solids (TDS) within groundwater, determine surface water salinity and the duration of water storage (Fig. 1A). For wetlands at high elevation groundwater discharge is less than groundwater recharge. This model predicts that high elevation wetlands will have low TDS inputs, low surface water salinity, and a short

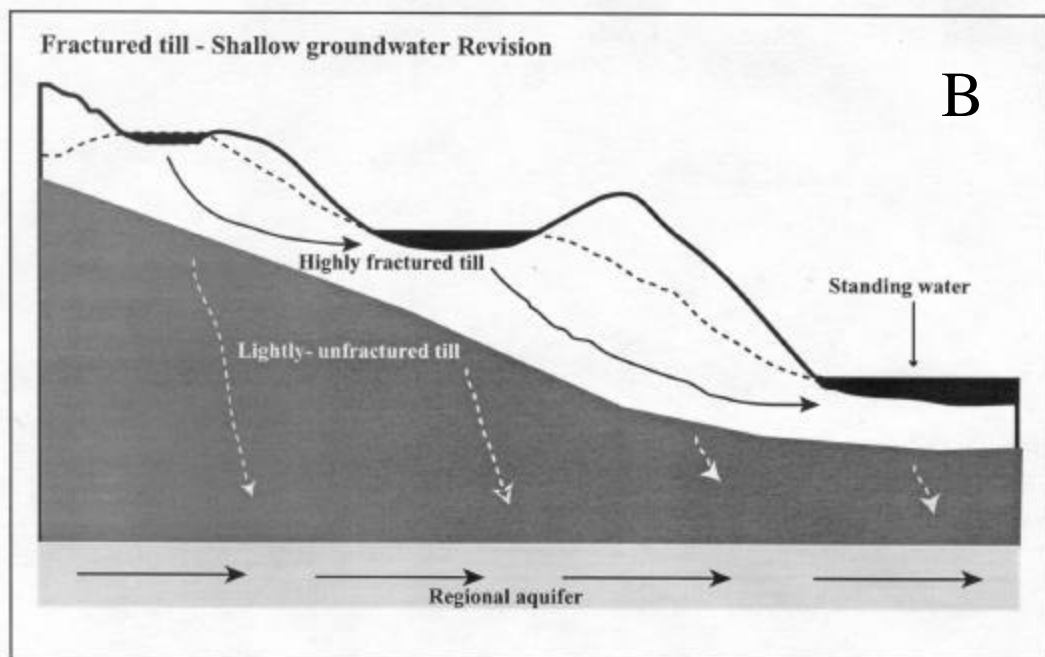
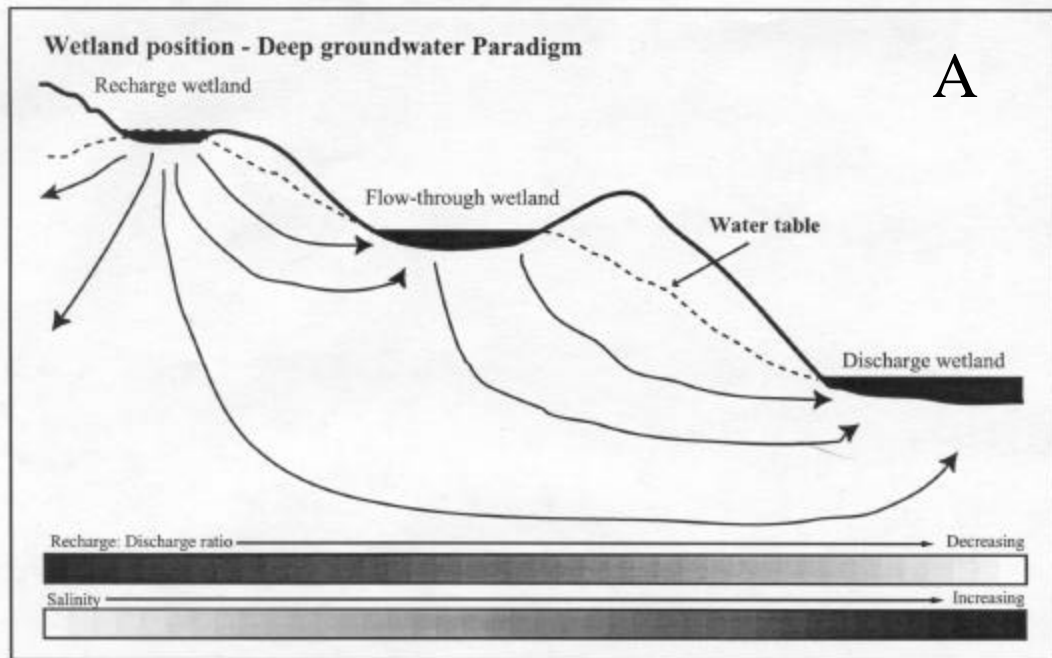


Figure 1. Generalized diagrams of (A) wetland elevation-groundwater interaction model (modified from Arndt and Richardson 1988), and (B) groundwater flow systems restricted by lightly fractured or unfractured till (modified from van der Kamp and Hayashi 1998). Dashed arrows indicate lower hydraulic conductivity in the less fractured till.

duration of inundation. Among wetlands at low elevations, groundwater discharge is greater than groundwater recharge. Therefore, the model predicts that low elevation wetlands will have high TDS inputs, high surface water salinity, and a long duration of inundation. Further, this model predicts that wetlands at intermediate elevations will have intermediate levels of TDS inputs, surface water salinity, duration of inundation, and both recharge and discharge groundwater in nearly equal amounts (i.e., flow-through wetlands). Although groundwater inputs are thought to make up a small portion of the total water budget of prairie potholes, their effects on water chemistry, hydrology, and vegetation are considered to be profound. Over the past three decades many studies have relied on groundwater connectivity to explain the variance in wetland surface water chemistry, vegetation composition, hydrologic regimes, and soil morphology and development (Stewart and Kantrud 1971 and 1972, Kantrud et al., 1989, Richardson and Bigler 1984, Miller et al., 1985, Mills and Zwarich, 1986, Arndt and Richardson 1988, Hubbard 1988, Richardson et al. 1994, Euliss and Mushet 1996, LaBaugh et al., 1998). However, Swanson et al. (1988) have shown there to be no relationship between elevation and salinity as an indicator of groundwater connection among the prairie potholes of central North America.

The deep groundwater connection model implies that the hydraulic conductivity of the glacial deposits underlying prairie potholes is spatially homogeneous. Van der Kamp and Hayashi (1998) challenged this view and suggested modifications to the groundwater connection model. They reported that the upper 4 m of the glacial deposits underlying prairie potholes are more highly fractured and have a higher mean hydraulic conductivity than deeper deposits. However, their description of hydraulic conductivity

did not distinguish between surface soils and underlying tills. Fractures in tills are due to alternating wet/dry and freeze/thaw conditions associated with climate phases and by the over-riding glaciers at the time of deposition (Haldorson and Kruger 1990). Van der Kamp and Hayashi (1998) suggested that groundwater connections among prairie potholes occur between the moist margins of wetlands within a few meters of the glacial till, where glacial deposits are fractured and have the highest hydraulic conductivity. They also suggested that only a small portion of groundwater recharge from wetlands enter deep regional flow pathways and aquifers. Figure 1B is an illustrated representation of the van der Kamp and Hayashi (1998) model. Their shallow groundwater perspective is a shift away from the deep groundwater connectivity model. However, it does not provide any explanation to why wetland elevation and salinity are not correlated in prairie potholes as observed by Swanson et al. (1988).

Many of the glaciated valleys of the Northern Rocky Mountains contain depressional wetlands structurally and geomorphically similar to the prairie potholes of central North America. However, alpine glaciers, rather than the continental ice sheets that formed the prairie potholes, formed the intermontane potholes. Incongruities to the groundwater-connectivity models, like the findings of Swanson et al. (1988), suggest that the importance of groundwater connections among wetlands may be over-emphasized and more information than elevation is needed to understand how depressional wetlands may be connected by groundwater flow systems.

In this study I examine the role of connectivity on wetland structure and function. In Chapter II, I examine the effects of groundwater inputs on selected characteristics of structure and function **within** intermontane depressional wetlands. In Chapter III, I

examine the effects of landscape level geomorphology, and surface and soil-water connections on the structure and function **among** intermontane depressional wetlands.

STUDY AREA

I conducted this research at the Bandy Experimental Ranch owned by The University of Montana (47° 3' 18'' N, 113° 14' W, ~1400 m). The Ranch is located in the Blackfoot Valley 80 km east of Missoula on the north side of the Blackfoot River (Fig. 2). The Blackfoot Valley has a Pacific maritime climate that is only occasionally dominated by continental air masses. Mean daily July maximum temperature and January minimum are 26 °C and –15 °C, respectively. Long-term mean annual precipitation (1976-1999) is 33.3 cm with 20.6 cm (62%) as rain during the growing season (April-September) and 12.6 cm (38%) as mostly snow in winter (October-March).

In the area of the Bandy Ranch, the Blackfoot Valley was occupied by a series of large alpine glaciers during the late Pleistocene (Dea 1981, Mudge et al. 1982, Alt and Hindman 1986). The last of these glaciers, the Monture advance, produced a stagnant glacier along its leading edge. This condition resulted in the deposition of disintegration moraines and outwash plains underlain by compacted till (Dea 1981). Dea (1981) and Mudge et al. (1982) described this compacted till as light brown to reddish brown clay to sand matrix with unweathered clasts of predominately quartzite-sandstone and argillite with very low abundance of limestone or dolomite. The surficial morphology of the Bandy Experimental Ranch is characterized by rolling hills, gentle sloping Palouse prairie grasslands, and a relatively high density of depressional wetlands. This study focused on the depressional wetlands of the South Pasture, a 130 ha area (W1/2, T. 15 N,



Figure 2. Geographical location map of the Bandy Experimental Ranch, Missoula, and Ovando, Montana.

R. 13 W) with a 100 m change in elevation along its long axis, north to south.

Approximately 110 depressional basins occur within the pasture, about 90 of which concentrate and store water for sufficient duration to have established hydrophytic vegetation and hydric soils. Although having a history of ranching and grazing, the South Pasture has remained in near pre-settlement (*circa* 1880) condition. Light grazing by livestock and the remote location of the South Pasture have served to preserve much of the South Pasture's ecological integrity. In addition to its particularly light landuse history, the South Pasture was not grazed for four years prior (1995-1998) or throughout the duration of this study (April-October 1999). Two features of the study site make it an ideal location for ecological study of intermontane depressional wetlands: (1) vegetation composition is dominated by native species, and (2) the north end of the pasture is the high point in the surrounding (4-5 km²) landscape. Thus, all local and regional groundwater and surface waters drain away from the South Pasture. These hydrogeomorphic characteristics negate potential local or regional surface water and groundwater depletions or contaminations.

The upland soils of the South Pasture were mapped (Soil Conservation Service 1995) as part of the Brazier-Perma-Water complex, with 8-25 % slopes. The Perma Series is cultivated. The Brazier Series is not cultivated and is classified as loamy-skeletal, mixed Pachic Argiborolls. These upland soils have a clay loam texture and range from 30-60 cm in depth to unweathered till.

CHAPTER II

Landscape processes determine spatial variation of structure and function *within* intermontane depressional wetlands: a reduced role for groundwater

OBJECTIVES

The objective of this research was to examine the effects of groundwater inputs on selected characteristics of structure and function within intermontane depressional wetlands. This research focused on the following questions derived from the contradictory hydrogeomorphic views found in the depressional wetland literature: (1) Is there evidence of groundwater inputs among depressional wetlands or are they isolated units on the landscape? (2) If there is no groundwater connectivity, is there another form of hydrologic connectivity? (3) Is there evidence that variation in landscape-level geomorphology and/or surface hydrology affects wetland structure and function locally within wetlands?

If groundwater connections occur among wetlands, it is reasonable to assume they will be spatially localized and selected characteristics of wetland structure and function will differ locally. In other words, the effects of groundwater connections among wetlands will be maximized between adjacent wetlands at connection points (i.e., “discharge” locations). In contrast, the effects of groundwater connections among wetlands will be minimized at non-connection points (i.e., “non-discharge” locations). To examine the assumptions of the groundwater connection model discussed in Chapter I, I compared spatially localized patterns and processes of near-surface water movement (i.e., soil water), soil development, soil water chemistry and nutrient availability, and

vegetation structure within intermontane depressional wetlands. If the groundwater-connectivity model is sufficient to explain the function of these wetlands, I expected to find (1) greater evidence of groundwater input at discharge locations than at non-discharge locations, (2) higher TDS (i.e., specific conductance and alkalinity) in near-surface water samples from discharge locations than at non-discharge locations, (3) stronger evidence of subsurface lateral water movement (i.e., eluviation in soil development by groundwater inputs) at discharge locations than at non-discharge locations, and (4) localized differences within wetlands in vegetation composition, coverage, diversity and productivity between discharge and non-discharge locations.

STUDY DESIGN

To test for local effects of groundwater discharge on wetland patterns and processes I used a natural “split-plot” design. I randomly selected 15 of the 90 depressional wetlands located in the South Pasture of the Bandy Ranch for this study (Fig. 3). “Plots” were the 15 wetlands, and “treatments” were different hydrogeomorphic locations within wetlands distinguished as groundwater discharge sites and non-discharge sites. I compared vertical hydrologic gradient (VHG), water chemistry, available N and P (as NO_3 and PO_4^-), soil development, and vegetation structure at discharge and non-discharge locations within the 15 study wetlands.

The concentrically banded herbaceous vegetation, characteristic of intermontane depressional wetlands, is a transitional pattern reflecting the moisture and elevation gradients that occur between the aquatic and terrestrial environments (Lesica 1994). Vegetation sampling plots, soil pits, and instrument (i.e., mini-piezometers and

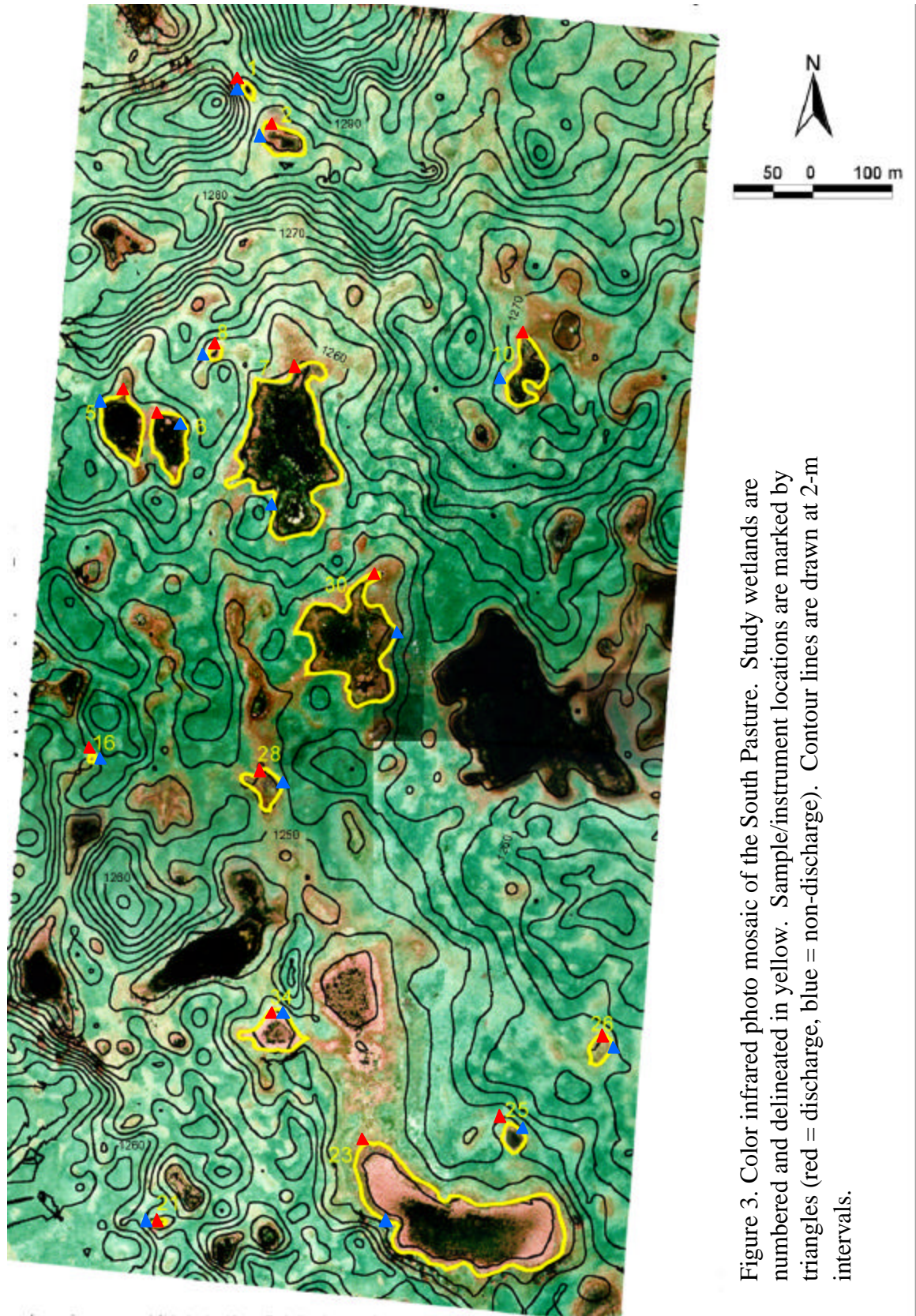


Figure 3. Color infrared photo mosaic of the South Pasture. Study wetlands are numbered and delineated in yellow. Sample/instrument locations are marked by triangles (red = discharge, blue = non-discharge). Contour lines are drawn at 2-m intervals.

lysimeters) placements were standardized so that they were within the uppermost vegetation community in each wetland. The upper vegetation community is usually inundated by standing water for 1-3 weeks immediately after spring snowmelt and is analogous to the “low-prairie” zone described by Stewart and Kantrud (1971 and 1972) and Kantrud et al. (1989). The herbaceous species *Deschampsia cespitosa*, *Agrostis scabra*, *Eleocharis palustris*, and *Potentilla anserina* commonly dominated this upper vegetation community, which I will refer to hereafter as the low-prairie.

Within wetlands, sampling sites also were standardized by elevation to control for the effects of standing water. I assumed the uppermost wetland vegetation community to be least affected by the physiological constraints of standing water and most responsive to groundwater discharge into the wetlands. Implicit in this assumption is that groundwater inputs intersect with the root zone (~1 m) of this upper vegetation community. This assumption is justified by personal observations that mean wetland depth (i.e., from upper wetland vegetation to maximum wetland depth) is ~1 m. Therefore, if groundwater does not intersect the root zone of the upper vegetation community, then it does not intersect the wetland either.

METHODS AND MATERIALS

Precipitation

Daily precipitation data were obtained from the Desert Research Institute-Western Regional Climate Center for Ovando, Montana (weather station 246304). It is located at the same elevation (1400 m) and ~15 km east-southeast of the Bandy Experimental Ranch.

Local hydrology

The flow rate (Q) of groundwater through any porous material is governed by Darcy's law where:

$$Q = K \times (\text{hydraulic gradient})$$

The constant K is the hydraulic conductivity and represents the permeability of the porous material. The hydraulic gradient is equal to the difference in hydraulic head along the flow path, divided by the length of the flow path (Fetter 1988). I did not assume Q , K , or the hydraulic gradient to be constant between wetlands or locations and did not attempt to standardize locations by vertical or horizontal distance between wetlands. Rather, I selected discharge locations on the hydrologic up-gradient side of all wetlands. Ten wetlands (2, 5, 6, 7, 8, 10, 23, 28, 30, and 34) were located at low to intermediate elevations in the South Pasture and discharge locations were selected on the side closest to its nearest hydrologically up-gradient neighboring wetland. Five wetlands (1, 16, 21, 25, and 26) were located at high elevations in the South Pasture and did not have hydrologically up-gradient neighboring wetlands. For these, discharge locations were selected on the wetland's elevational and topographical high side in relation to the long axis of its catchment. All non-discharge locations had no other wetland adjacent to that side and were perpendicular to suspected groundwater flow pathways and discharge locations. I observed that discharge locations were morphologically concave and non-discharge locations were convex.

Groundwater movement in and out of wetlands was determined by measuring the differences in elevations (i.e., vertical hydraulic gradient or VHG) between the standing water in the wetland and water table in the root zone of the low-prairie. I compared

seasonal patterns of VHG from weekly measurements between discharge and non-discharge locations. Staff gauges were used to measure standing water elevations in wetlands and nested mini-piezometers were used to measure soil water elevations. Mini-piezometers were constructed from 2.5-cm diameter PVC pipe and had cone-shaped nylon tips in the lower end. The mini-piezometers were perforated with 2-mm holes on four sides every 1 cm along the bottom 10 cm of the pipes. Two mini-piezometers were installed as pairs at each sample location, one to a depth of 40 cm, and the other to 80 cm. Piezometers were installed with a sliding-hammer driver that slides into the piezometer and installs the piezometer with minimal soil disturbance. Paired mini-piezometers were placed 20 cm apart at all locations. Staff gauges and mini-piezometer locations were surveyed using a Leica TC600, Total Survey Station. All measurements were corrected to a standard datum elevation for analyses.

Soils

I investigated the long-term differences in environmental conditions between discharge and non-discharge locations by examining soil development from soil pits. I measured soil O-, A- and E-horizon thickness, and overall soil depth (to the C-horizon), soil texture, and described the distribution of calcium carbonate (CaCO_3) and redoximorphic features throughout the soil profiles.

The soil O-horizon is the accumulation of decomposing organic material (largely plant litter). Organic materials accumulate in wetland soils as a result of anaerobic conditions created by standing water or poorly drained conditions. Therefore, the thickness of the O-horizon reflects the historical balance between productivity and

decomposition at that location (Brady 1984, Soil Survey Division Staff 1993). The soil A-horizon is a surface mineral soil layer characterized by the accumulation and incorporation of humified organic material into the mineral soil. The thickness of the A-horizon reflects the degree of soil development and the depth to which organic materials have been translocated by water moving through the soil (Brady 1984, Soil Survey Division Staff 1993). The soil E-horizon is a subsurface mineral soil layer characterized by eluviation (leaching out) of soluble soil constituents like salts, CaCO_3 , organic material, clay, and iron (Brady 1984, Soil Survey Division Staff 1993). E-horizons can form by a complex process termed ferrollysis (Brinkman 1970) in soils with fluctuating water tables and barriers that impede the downward movement of water (e.g., parent materials of compacted till). The fluctuating water table causes alternating oxidation and reduction in the overlying soil so that the iron alternates between the Fe^{2+} and Fe^{3+} state. During reduced conditions Fe^{2+} is mobile and it and the other soluble constituents are leached from the soil by laterally moving waters over the impermeable layer (Brinkman 1970, Birkland 1984, and van Breeman 1988). Under these conditions the development of an E-horizon reflects a dominance of lateral, rather than vertical, water movement through the soil. Soil B-horizons are a subsurface mineral soil layer characterized by the illuvial accumulation of salts, CaCO_3 , silicate clays, and iron from overlying soils. The development of a B-horizon reflects a dominance of vertical, rather than lateral, water movement through the soil. The C-horizon (soil parent material) is technically not part of the solum (i.e., the upper weathered soil) and by definition has been little affected by soil forming processes. However, water movement into and through the soil has a great effect on soil development and the depth to which soil weathering takes place. The upper layers

of the C-horizon, over time, undergo transformation to become part of the overlying soil as weathering processes continue. Therefore, the depth to the C-horizon reflects the extent of soil development (Brady 1984, Soil Survey Division Staff 1993).

Calcium carbonate (CaCO_3) is a soluble soil constituent, as are salts and silicate clays. The accumulation of CaCO_3 reflects the processes of leaching and translocation caused by water moving downward through the soil. The degree of CaCO_3 accumulation is categorized by its effervescent reaction (i.e., none, weak, moderate, and strong) to a 10% hydrochloric acid solution (Soil Survey Division Staff 1993). I recorded the depth and expression of effervescence of CaCO_3 where they occurred in the solum at each location.

Soil texture was determined by the feel method (Soil Survey Division Staff 1993). I determined the soil texture for each soil horizon found at each location. Soil redoximorphic features (i.e., indicators of hydric soils or anaerobic conditions that result from repeated periods of saturation or inundation for more than a few days) are common to wetland soils (Vepraskas 1994, NRCS 1996). I described soil redoximorphic features following the methods of NRCS (1996).

I also observed a series of soil profiles by coring through the weathered soil to the compacted glacial till at the site of maximum water depth within wetlands. Soil cores were taken with a 2.0-m length soil auger. The cores were field evaluated for the moisture content and depth to the unweathered glacial till. Observations from these deeper cores within the wetlands allowed me to evaluate the likelihood of groundwater connection through the compacted till between wetlands.

Vegetation structure

Species composition and total aerial coverage for all species were recorded from three plots located immediately adjacent to piezometers in mid-July 1999. I used a 1.0 m x 0.5 m quadrat for all plots with the long axis oriented parallel to the concentric banding of vegetation to reduce sampling bias of the often narrow (<1.0 m) low-prairie community that encircled each depressional wetland. For each location, mean species composition and coverage from the three plots were used for analysis. Mean species richness and evenness (Pielou 1969) were also calculated from the composition/coverage data.

I calculated net primary productivity as above-ground plant biomass produced during the growing season of 1999. Biomass samples were collected in early October 1999 to ensure an accurate measure of productivity for the growing season. The current year's vegetation (i.e., less the prior year's detritus) was clipped and bagged from two micro-plots (0.1 m²) located randomly within 1 m of the piezometers at each sampling location. Samples were dried at 60°C for 72 h and weighed (\pm 0.01 g). Net primary productivity was calculated as the mean value of the two samples taken at each location and converted to kg/m².

Soil water chemistry and nutrient availability

I sampled near-surface soil water from lysimeters installed at each discharge and non-discharge location in all study wetlands. All lysimeters were installed adjacent to piezometers at all locations and to a standard depth of 50-cm. Lysimeters were constructed of 9-cm diameter PVC pipe cut to a length of 30 cm. Lysimeters were

perforated on four sides with 2 x 10-mm slots every 1 cm along their length. Each had a polystyrene cap at the top and bottom and was fitted with a length of 10-mm diameter nylon tubing that reached from the bottom of the lysimeters to 30 cm above the soil surface. The tubing was capped until water samples were extracted. Holes for the lysimeters were dug with a 7.6-cm diameter soil auger, which minimized soil disturbance and insured a snug interface between the lysimeters and surrounding soil. After the lysimeter was installed the remaining hole was backfilled with the soil removed by the auger. Lysimeters were installed on May 25, 1999, allowed to equilibrate for 7 days, and evacuated using a peristaltic hand pump. Lysimeters were left to equilibrate again for 7 days before sampling in late spring (June 8) and summer (July 6) of 1999. The hose of the peristaltic hand pump used to extract water samples was rinsed 3-times with de-ionized water before each sample acquisition at each location.

Dissolved oxygen (DO), pH, and specific conductance (SpC) were measured in the field using a multi-probe Hydrolab Surveyor-3. I collected water samples for water chemistry following standard methods of APHA (1992) with minor modifications (Stanford et al. 1986) for soluble reactive phosphorus (SRP), nitrate plus nitrite ($\text{NO}_3 + \text{NO}_2$), and carbonate alkalinity. Nitrate and SRP samples were prepared by centrifugation for 4 minutes at 1500 rpm to remove suspended sediment (>1 micron). Water samples were then filtered through a 0.45-micron filter, per standard methods for dissolved nutrients, then frozen for later analysis at the Flathead Lake Biological Station's freshwater research laboratory.

Data analysis

I performed all data analyses using SPSS for Windows 8.0 (SPSS 1997) and PC-ORD (McCune and Mefford 1999). I considered test results to be significant at $\alpha = 0.05$ and report all p-values. A two-way Analysis of Variance (ANOVA) procedure was used to compare water chemistry and nutrient levels between sampling dates and hydrogeomorphic locations when data met assumptions of normality and homogeneity of variance. Mean values represent $n = 15$ discharge and $n = 15$ non-discharge locations for June 8, 1999 data and $n = 11$ discharge and $n = 14$ non-discharge locations for July 6, 1999 data (lysimeters at four discharge and one non-discharge location were dry on July 6, 1999). DO, SpC, and alkalinity data were (\ln) transformed and PO_4^- data were ($\sqrt{\ln}$) transformed to meet assumptions of normality and homogeneity of variance. Many NO_3 measurements were below detection limits ($0.6 \mu\text{g/L}$). For samples below detection limits I used the value $0.6 \mu\text{g/L}$ in analysis. However, the NO_3 data could not be transformed to meet assumptions of normality and were imbalanced between dates, which prevented any meaningful statistical analysis. For all data, I present means and 1 SE.

The VHG data did not meet assumptions of sphericity required for repeated measures ANOVA for comparing weekly measurements between discharge and non-discharge locations. I present weekly mean VHG (± 1 SE) for discharge and non-discharge locations throughout the growing season.

Mean soil A-horizon thickness, depth to C-horizon and net primary productivity between discharge and non-discharge locations were compared using independent samples t-tests when data met assumptions of normality and homogeneity of variance. I

used the Mann-Whitney's non-parametric test to compare mean soil O-horizon thickness between discharge and non-discharge locations when the data could not be transformed to satisfy the assumptions for parametric tests.

I evaluated species composition and coverage for discharge and non-discharge locations using PC-ORD (McCune and Mefford 1997) and the multivariate technique of detrended correspondence analysis (DCA). The primary matrix used for analysis was developed from the plant composition and coverage data described above. The primary matrix included species composition and coverage data from each of the 30 locations (i.e., 15 wetlands x 2 hydrogeomorphic locations per wetland).

RESULTS

Precipitation

Annual precipitation for 1998 was 41.5 cm, making that year wetter than the long-term average of 33.3 cm (Fig. 4). In contrast, annual precipitation for 1999 was 27.3 cm, making that year slightly drier than the long-term average.

Local hydrology

I did not detect any evidence of groundwater inputs. Vertical hydraulic gradient within wetlands varied substantially through time (Fig. 5). However, seasonal patterns of VHG were not different between discharge and non-discharge locations. For all study wetlands and locations within wetlands, standing water recharged bank storage during spring (-VHG), was neutral in early summer, but reversed flow from the bank into the wetland (+VHG) by early July and continued for the remainder of the growing season. At 40-cm depth, VHG was negative from late April until early June, neutral until July,

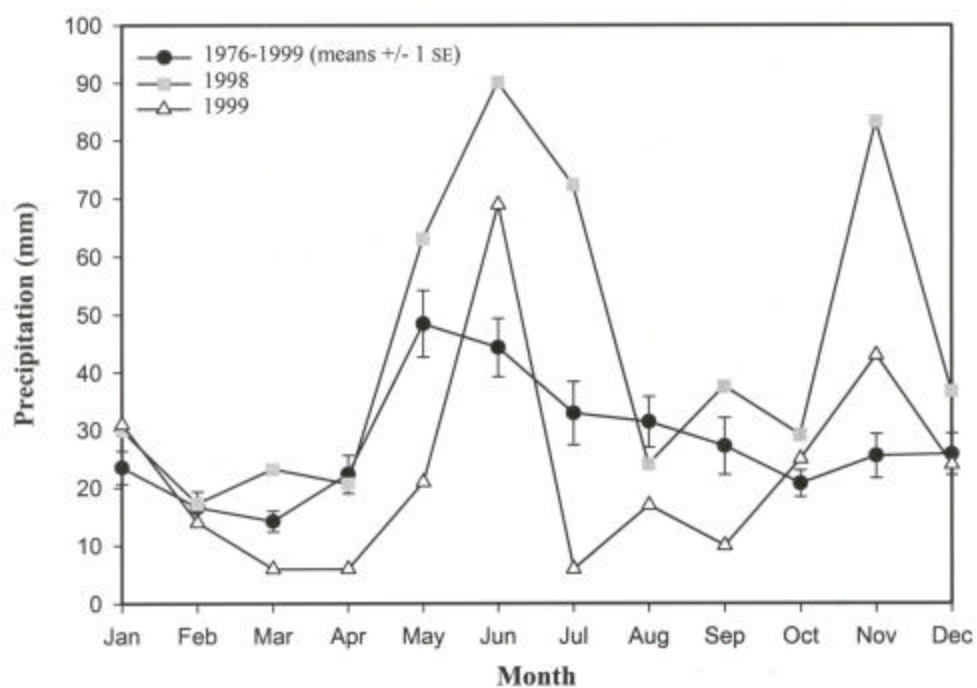


Figure 4. Monthly precipitation for 1998 and 1999 and monthly means (\pm 1 SE) for the period of record (1976-1999).

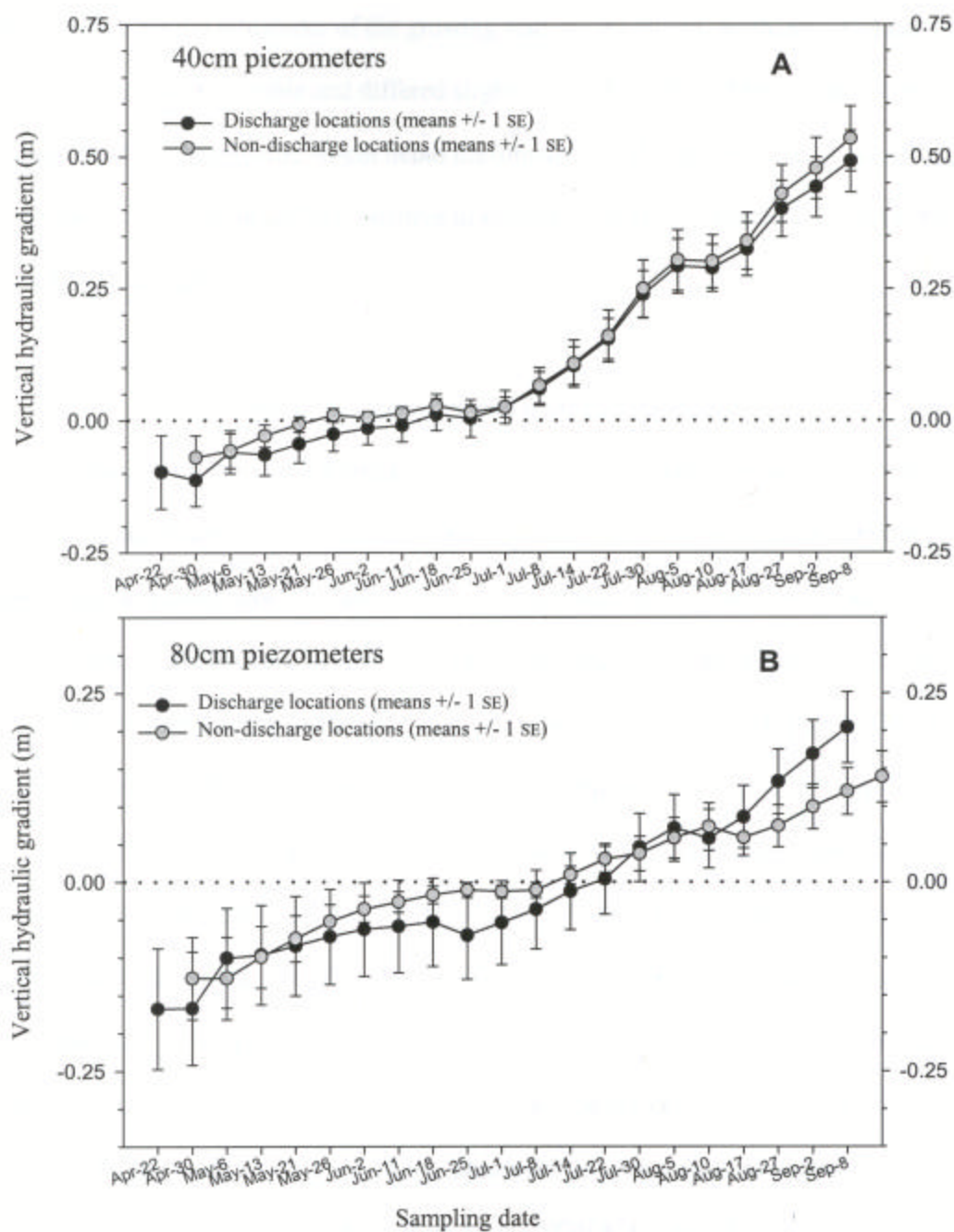


Figure 5. Weekly vertical hydraulic gradient for (A) 40cm piezometers and (B) 80cm piezometers for discharge and non-discharge locations within wetlands.

and positive for the remainder of the growing season. At 80-cm depth, seasonal patterns of VHG were more variable and differed slightly in magnitude and timing from the pattern observed among the 40-cm depth piezometers. VHG at 80-cm depth was slightly more negative in spring and less positive in summer, and flow reversed 2-3 weeks later than at 40-cm depth.

Soil-water chemistry and nutrient availability

Sampling dates (June 8 and July 6, 1999) coincided with neutral and positive VHG (i.e., soil water moving into the wetland) measurements, respectively. However, I found similar values between dates for all six of the variables I measured. Alkalinity and SpC varied greatly between discharge and non-discharge locations, but in contrast to the groundwater-connectivity model, non-discharge locations were more highly buffered than discharge locations, and tended to have higher concentrations of dissolved salts (Fig. 6). Mean alkalinity was 3 times higher at non-discharge locations than discharge locations (two-way ANOVA, $F = 3.8$, $df = 1, 54$, $P = 0.055$), but there was no difference between dates (two-way ANOVA, $F = 0.4$, $df = 1, 54$, $P = 0.592$). Mean SpC was not different between locations (two-way ANOVA, $F = 1.5$, $df = 1, 54$, $P = 0.223$) or dates (two-way ANOVA, $F = 0.2$, $df = 1, 54$, $P = 0.620$). Mean values for DO and pH varied little among locations and dates (Fig. 6). Dissolved oxygen values were low overall and were not different between locations (two-way ANOVA, $F = 0.2$, $df = 1, 54$, $P = 0.649$), or dates (two-way ANOVA, $F = 0.7$, $df = 1, 54$, $P = 0.394$). Near-surface waters at discharge and non-discharge locations were neutral to very slightly acidic and were not

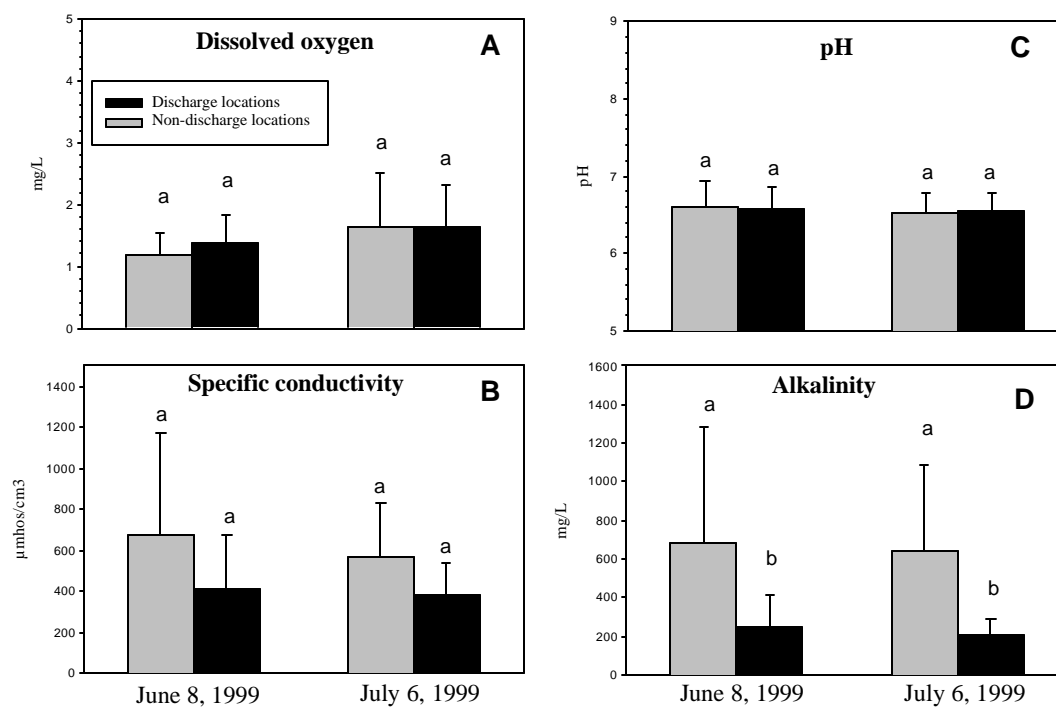


Figure 6. Means (+ 1 SE) for A) dissolved oxygen, B) specific conductivity, C) pH, and D) Alkalinity at discharge and non-discharge locations within wetlands on June 8, and July 6. Treatments with different letters within a panel are statistically different at $P < 0.1$ level.

different between locations (two-way ANOVA, $F = 0.01$, $df = 1, 54$, $P = 0.932$) or dates (two-way ANOVA, $F = 0.1$, $df = 1, 54$, $P = 0.732$).

Available NO_3 and SRP were very low and varied little across all locations and dates (Fig. 7). NO_3 measurements were often below detection limits (0.6 ug/L). Thirty-five samples (17 at discharge and 18 at non-discharge locations), out of all 54- NO_3 samples ($n = 30$ from June 8 and $n = 25$ from July 6) were below detectable limits and prevented any meaningful statistical analysis. In contrast, PO_4^- measurements were always above detection limits (0.4 ug/L), but mean values were low overall (total mean = 1.3 ug/L) and did not differ across locations (two-way ANOVA, $F = 0.29$, $df = 1, 54$, $P = 0.592$) or dates (two-way ANOVA, $F = 0.48$, $df = 1, 54$, $P = 0.492$).

Soil development

Soil E-horizons were conspicuously absent at all locations. Soil development was greater at discharge locations than at non-discharge locations, despite there being no difference in elevation between discharge and non-discharge locations within wetlands. Overall mean soil depth (i.e., depth to C-horizon) was greater at discharge locations than non-discharge locations ($t = 2.455$, $df = 28$, $P = 0.021$; Fig. 8) and soil O-horizons were thicker at discharge locations than at non-discharge locations ($T = 278.0$, $P = 0.061$). However, there were no differences in A- horizon thickness between discharge locations and non-discharge locations ($t = 1.535$, $df = 28$, $P = 0.136$; Fig. 8).

Soil textures increased in clay content with depth at all locations. Soil textures of A- and C-horizons varied little between discharge and non-discharge locations, but soil textures tended to have higher clay content at discharge locations than at non-discharge

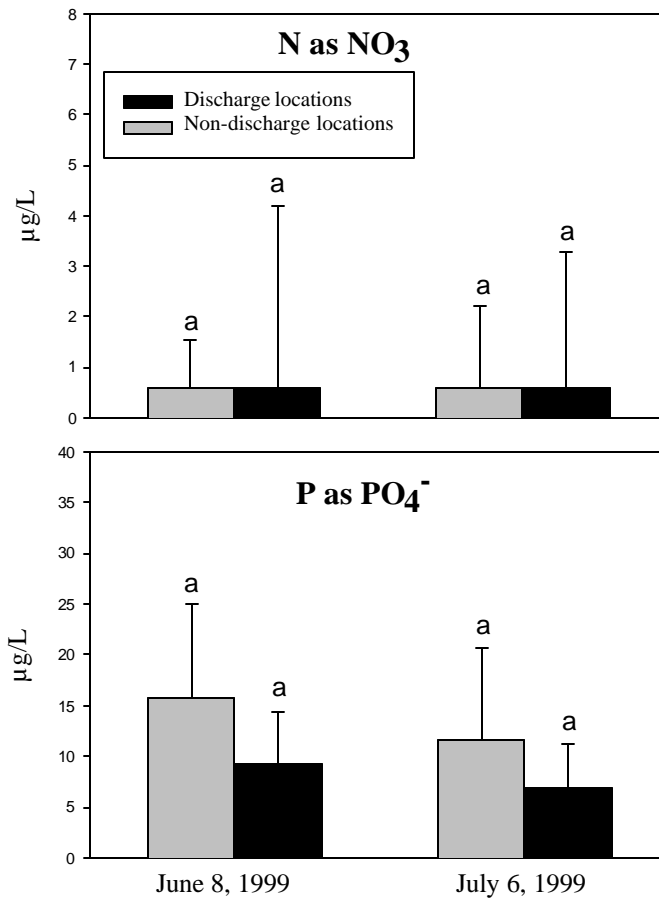


Figure 7. Means (+ 1 SE) for A) nitrate plus nitrite, and B) soluble reactive phosphorus (SRP) at discharge and non-discharge locations within wetlands on June 8, and July 6. Treatments with different letters within a panel are statistically different at $P < 0.1$ level.

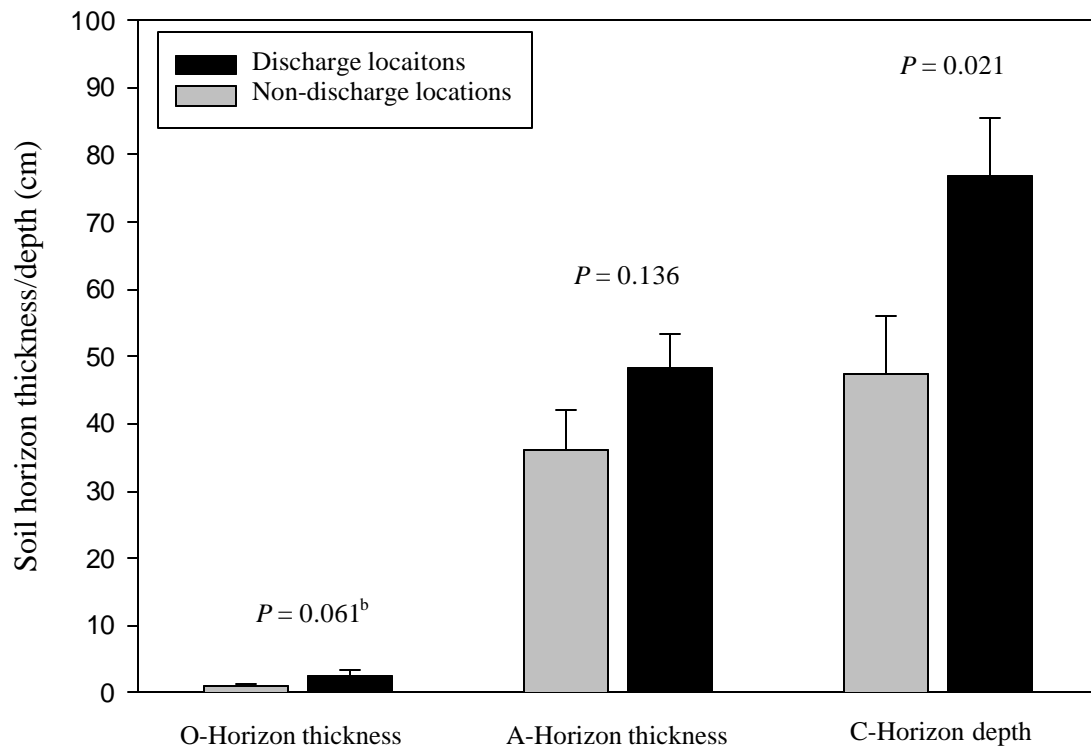


Figure 8. Mean (+ 1 SE) soil O- and A-horizon thickness and depth to C-horizon for discharge and non-discharge locations within wetlands. ^b = Mann-Whitney nonparametric test.

locations. Soil texture for all A-horizons were silt-loam. Soil textures for C-horizons were silty-clay-loam and occasionally clay-loam for all locations. Subsurface soil horizons across all locations were B-horizons, not the anticipated E-horizons. This indicated illuvial accumulations of silicate clay and humified organic material from overlying soil, rather than the loss of these same materials by eluviation (i.e., the leaching or removal of clay and organic matter). Between locations, B-horizons showed greater evidence of the translocation of clay at discharge locations than non-discharge locations. Soil texture increased in clay content from silt-loam to silty-clay-loam at 8 of the 15 discharge sites. No difference in soil texture was discernable at the other 7 discharge locations nor at any of the non-discharge locations.

The presence and distribution of CaCO_3 in soil profiles did not reflect any discernable pattern between discharge and non-discharge locations. CaCO_3 was present in only 9 of the 30 soil profiles, 4 of 15 discharge locations and 5 of 15 non-discharge locations.

Similarly, apart from the presence/absence and thickness of soil O- and A-horizons (described above), the presence, distribution and type of soil redoximorphic features did not reflect any discernable pattern between locations within wetlands. Specifically, I found a paucity of soil redoximorphic features present within the mineral soils, yet they occurred equally across locations (i.e., 8 of 15 discharge and 8 of 15 non-discharge locations).

Vegetation structure

Discharge locations were 25% more productive than non-discharge locations ($t = 2.58$, $df = 28$, $P = 0.015$, Fig. 9). However, hydrogeomorphic location had no effect on species composition, coverage, or diversity within a wetland. Species richness was 49 across all wetlands and locations. Alpha diversity for discharge and non-discharge locations was 41 and 45 species, respectively. The number of species found exclusively at discharge and non-discharge locations was 4 and 8, respectively. All species found exclusively at either discharge or non-discharge sites had frequencies of occurrence of ≤ 2 of the 15 locations, except that *Sisyrinchium angustifolium* (Blue-eyed grass) was found at 4 of the 15 non-discharge locations. *Grendelia howellii* (Howell's gumweed) species considered very rare globally (G3) and very rare (S3) and imperiled (S2) in Montana (MNHP 2001) was found at only 1 non-discharge location. Mean species richness (discharge = 12.4, non-discharge = 13.3) and evenness (discharge = 0.70, non-discharge = 0.74; Pielou 1969) did not differ between discharge and non-discharge locations ($t = -0.94$ $df = 28$, $P = 0.370$ and $t = -1.05$, $df = 28$, $P = 0.304$, respectively).

DCA ordinations indicated that vegetation composition was similar at discharge and non-discharge locations (Fig. 10). Mean ordinal scores for discharge and non-discharge sites did not differ ($t_{\text{Axis 1}} = 0.587$, $df = 28$, $P = 0.562$ and $t_{\text{Axis 2}} = 0.525$, $df = 28$, $P = 0.604$).

Neither hydrogeomorphic location type was characterized by a particular species or growth-form. The ten most abundant species at both discharge and non-discharge locations was a mix of grasses, sedges, and forbs (Table 1). The mean coverage of dominant species ranged from 12.7 - 3.7%.

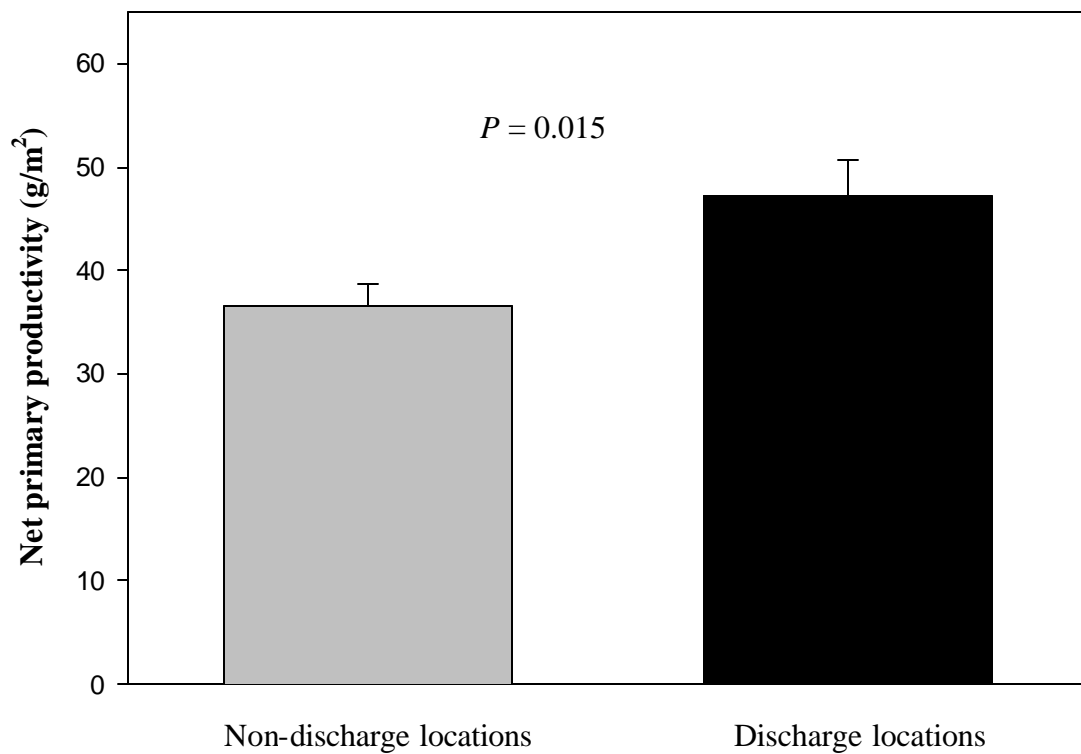


Figure 9. Mean (+ 1 SE) net primary productivity for discharge and non-discharge locations within wetlands.

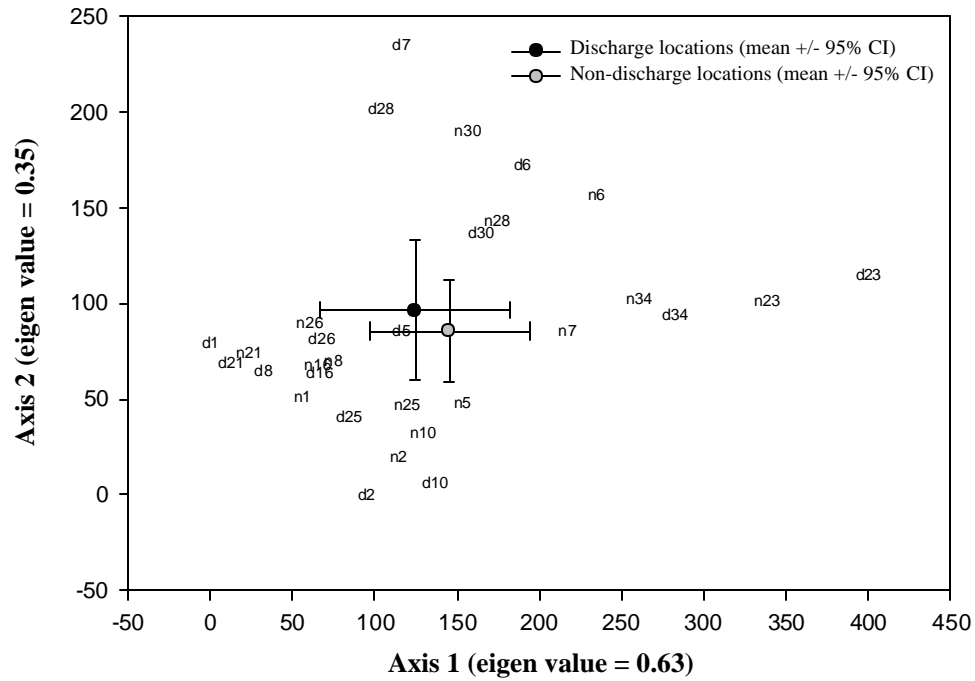


Figure 10. Detrended correspondence analysis (DCA) of groundwater discharge and non-discharge locations within wetlands using macrophyte species composition and coverage data. Mean ordinal location scores (\pm 95% confidence intervals) for Axis 1 and 2 are shown. Alpha-numerics represent groundwater treatment and study wetland (e.g., d7 = discharge location in wetland 7).

Table 1. The ten most abundant macrophyte species at discharge and non-discharge locations within wetlands. Species are presented in order of total abundance across both locations.

Species	Percent Coverage			
	Discharge locations		Non-discharge locations	
	Mean (1 SE)		Mean (1 SE)	
1. <i>Potentilla anserina</i>	13.9	(2.1)	11.5	(3.7)
2. <i>Deschampsia cespitosa</i>	14.1	(4.6)	9.8	(3.3)
3. <i>Juncus baliticus</i>	10.6	(3.4)	13.2	(4.3)
4. <i>Agrostis scabra</i>	6.3	(1.7)	14.4	(2.9)
5. <i>Eleocharis palustris</i>	10.5	(3.7)	9.4	(2.4)
6. <i>Carex lasiocarpa</i>	8.2	(5.9)	5.6	(2.8)
7. <i>Mentha arvensis</i>	3.7	(1.6)	5.7	(1.5)
8. <i>Carex athrodes</i>	2.7	(0.8)	5.2	(1.9)
9. <i>Carex praeacilis</i>	5.6	(3.9)	1.8	(1.0)
10. <i>Phleum pratense</i>	4.5	(1.3)	2.8	(1.1)

DISCUSSION

My results indicate that deep groundwater connections were extraordinarily weak or did not occur, and that surficial landscape morphology and surface/near-surface hydrology are of primary importance to the structure and function of intermontane depressional wetlands. Three lines of evidence indicate that the intermontane potholes studied here were functionally “perched”. In other words, groundwater plays a minimal role in intermontane depressional wetland hydrology. First, seasonal patterns of VHG did not differ between discharge and non-discharge locations. Second, soil development at wetland margins provided no evidence of lateral subsurface water movement into wetlands as evidenced by the absence of E-horizons. Third, soil cores taken from the center of the wetlands, without exception, contained decreasingly weathered compacted till that became drier with depth to ~2 m below the soil surface.

The lack of a difference in seasonal patterns of VHG between discharge and non-discharge locations indicates that groundwater inputs were not detected. However, the VHG results were limited to one year and 1999 was drier than normal. Below-normal precipitation could have resulted in below-normal groundwater recharge from adjacent wetlands and therefore no difference in VHG between discharge and non-discharge locations. However, the climate data, as they relate to wetland hydrographic storage and potential groundwater connections, suggest that discharge was not limiting in 1999. Hydrographic storage for prairie potholes (Shjeflo 1968, Eisenlohr 1972, Winter et al. 1984, Hubbard and Linder 1986, Winter and Woo 1990, LaBaugh et al. 1998) are known to be greatest in spring as a result of overwinter precipitation and spring runoff. Precipitation in the five months during the preceding winter (October 1998-March 1999)

received greater than normal precipitation (Fig. 4). Therefore, initial hydrographic storage was probably higher than normal, and precipitation was not likely to be limiting to groundwater interactions between wetlands. The groundwater-connectivity model predicts a steeper hydraulic gradient between the near-surface water table depth in the low-prairie and the standing water in the wetland at discharge locations than at non-discharge locations. This prediction would have resulted in a greater and more positive mean weekly VHG at discharge locations than at non-discharge locations. This predicted pattern was not observed at either 40-cm or 80-cm depth. Therefore, groundwater inputs were not detected at discharge locations. I interpret the seasonal patterns of VHG (i.e., negative in the spring, neutral in mid-summer, and positive in late summer) among discharge and non-discharge locations as exchange of water between bank storage and standing water in the wetlands. Specifically, the soils beneath the low-prairie were recharged from standing water in the wetland in spring. Then as standing water in the wetland declined over summer the water stored in the bank was discharged back into the wetland. A schematic representation of this pattern is presented in Figure 11.

Brinkman (1970), Birkland (1984), and van Breemen (1988) described the three conditions necessary for ferrolysis and the development of a soil E-horizon: 1) a less permeable substrate, 2) a high local water table, and 3) laterally moving subsurface waters. Soil E-horizons were not found at any of my discharge or non-discharge locations. Moreover, subsurface soils at all locations were B-horizons characterized by the illuvial accumulations of silicate clays from overlying soils. The absence of E-horizons, and the presence of B-horizons, indicated that lateral groundwater inputs to

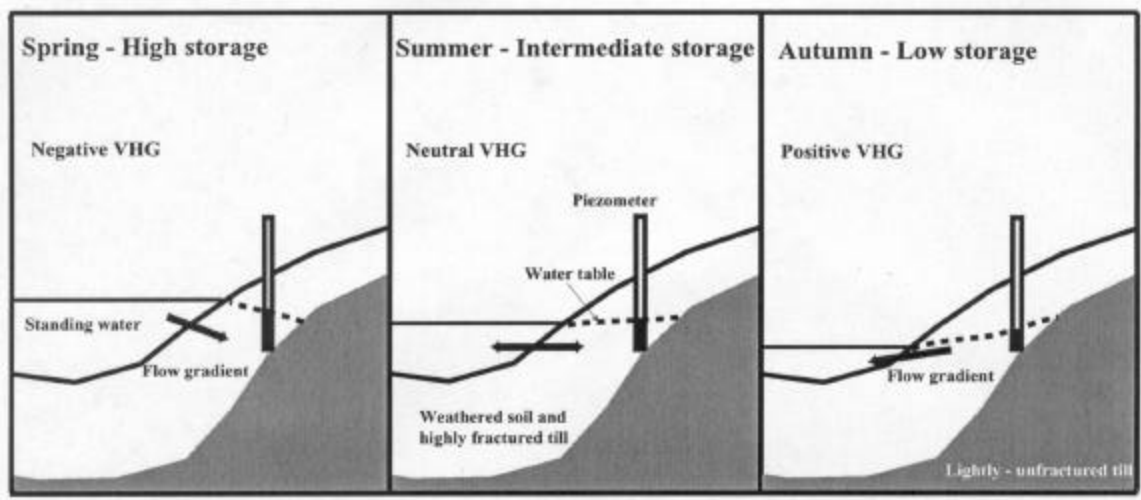


Figure 11. A schematic illustration of the seasonal changes in vertical hydraulic gradient at margin of a depressional wetland.

wetlands, above the compacted glacial till, were minimal, compared to downward water movement, or non-existent.

The dry soil cores and the unaltered parent material taken from beneath the center of wetlands strongly indicated that my study wetlands were not contributing water to groundwater or were connected to other wetlands through the compacted glacial till. The unweathered, dry glacial till underlying the South Pasture in the uplands as well as immediately below these wetlands suggests that groundwater plays a minimal role in the hydrology of these wetlands and that if hydrologic connections occur between wetlands, they must be dominated by surface or near surface pathways within the weathered soil.

Rather than being driven by groundwater hydrology, my results for soil development, primary productivity, water chemistry, and geomorphology indicate that landscape morphology and surface hydrology are the dominant factors in depressional wetland structure and function. First, higher alkalinity and the trend toward higher specific conductance at non-discharge locations than at discharge locations are opposite the predictions of the groundwater-connectivity model. Second, discharge locations were geomorphically positioned at the base of more concave slopes, whereas non-discharge locations were positioned at the base of convex slopes. Third, despite groundwater discharge and non-discharge sites being at the same elevation within wetlands, soil development and above-ground productivity were greater at discharge locations than at non-discharge locations.

The groundwater-connectivity model predicted TDS at discharge locations would be greater than at non-discharge locations. I found the opposite. Stolte et al. (1992) showed that the development of salinity is almost exclusively due to the transport of salts

by capillary soil moisture flow from standing water in the wetland to the root zone at the wetland margin. The hydrologic gradient between the standing water and the soils at the wetland margin is generated by high evapotranspiration demands from vegetation particularly during midsummer months when bank storage is declining (Stolte et al. 1992). Therefore, salinity should be high around the wetland margin except where the concentration and infiltration of surface waters occurs and has a “flushing” effect on soil salinity. The lower alkalinity and the lower trend in SpC of near-surface water at discharge locations than at non-discharge locations was evidence for greater localized concentration of “freshwater,” by catchment morphology.

Catena theory (i.e., the study of pedogenic processes responsible for the lateral variability of soils on a hillslope) for dry climates indicates that soil development is spatially variable where deeper soils are found at topographically low positions on the landscape (Birkland 1984). Deeper soils are the result of weathering of the underlying material *in situ* and erosional deposition. Holding soil-forming factors like time and parent material constant, soil weathering in dry climates is largely driven by greater soil moisture and the downward movement of water through the soil (Birkland 1984). Therefore, a deeper soil is due to greater soil moisture and water movement, which are largely determined by slope position. Soils in the South Pasture were shallow and weakly developed at hilltops (Soil Conservation Service 1995), and were deeper and well developed at the wetland margins (Fig. 8). Discharge and non-discharge locations were at similar topographic footslope-positions within each wetland, and it is reasonable to assume that the soil parent materials at the same elevation within a basin were the same age. However, discharge locations within each basin tended to be positioned at the base

of concave slopes, whereas non-discharge locations were positioned at the base of convex slopes. Since, overland flows are driven by surficial morphology and concentrated at topographic lows, surface water inputs should have been greater at discharge locations than at non-discharge locations. Greater overall soil development (Fig. 8), the greater depth to the C-horizon, thicker O-horizons, and the trend of higher accumulations of illuvial clay in B-horizons are all strong evidence for greater long-term water availability at the surface and water movement vertically through the soil at discharge locations than at non-discharge locations. These results indicate that landscape-level processes observed in this study create localized differences in soil water chemistry and soil development.

Many studies (Stewart and Kantrud (1971 and 1972, van der Valk and Davis 1978, Galatowitsch and van der Valk 1996) have described and modeled (van der Valk 1981) vegetation zonation in prairie wetlands along elevation and hydrologic gradients, but none of these studies address variation in vegetation composition at wetland margins in relation to catchment morphology or surface hydrology. I observed higher vegetative productivity at discharge locations than at non-discharge locations (Fig. 9). This may have been due to the greater water availability at discharge locations derived from surface water inputs or from the physiological constraints on growth resulting from higher salinity at non-discharge locations.

Considered together, my results provide strong evidence that groundwater has little affect on the hydrology and salinity of intermontane depressional wetlands. These results conflict with classic groundwater-connectivity models for prairie pothole wetlands (i.e., Sloan 1972, LaBaugh et al. 1987, Arndt and Richardson 1989, Richardson et al.

1992, and van der Kamp and Hayashi 1998). Overland-flow concentrated by catchment morphology and temporary surface or soil water connections between wetlands appears to have a proximal effect on the structure and function of intermontane wetlands.

If hydrologic connections occur between intermontane depressional wetlands, they depend on catchment geomorphology and are restricted to topographic lows and to the weathered soil (Fig. 12). Likewise, spatial barriers to surface water and soil water connections will occur between wetlands at topographic highs where soil development and unweathered till are the shallowest. Because surface water connections between wetlands only occur when elevations of stored surface water are greater than the surrounding topography, these spatial barriers also temporally restrict hydrologic connections between wetlands. Similarly, soil water connections occur only when shallow water tables are higher in elevation than the elevation of the unweathered till barrier. These surface connections may have large effects on the function of wetland ecosystems and understanding their role contributes to an emerging picture that emphasizes the importance of landscape-scale processes on the structure and function of wetland ecosystems. If landscape-scale processes are important even to the function of small, apparently simple wetlands, current policy on wetland conservation and management should be revised.

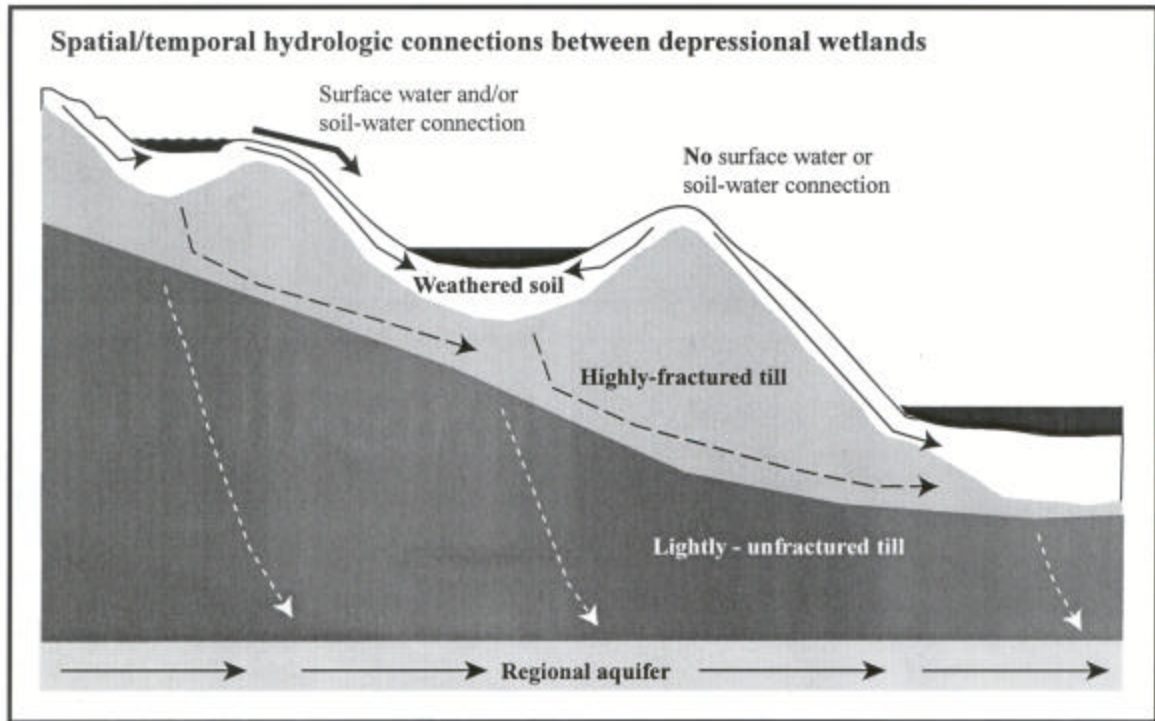


Figure 12. Generalized diagram of how spatial variation in topography and soil development/till fracturing can affect spatial and temporal hydrologic connections of surface waters and shallow groundwater between depressional wetlands on the landscape.

CHAPTER III

Landscape geomorphology and hydrologic processes determine the structure and function *among* intermontane depressional wetlands

OBJECTIVES

The objective of this research was to determine the effects of landscape geomorphology and surface and soil-water connections on the structure and function of intermontane depressional wetlands. Because depressional wetlands are found in topographic basins, they are collection areas for catchment-wide or “off-site,” indirect surface and soil-water inputs. In Chapter II, I showed that intermontane depressional wetlands lack deep groundwater connections. I also observed that within catchment morphology plays a major role in the spatial and temporal quantity and quality of water inputs and affects soil salinity, soil development, and vegetation productivity within wetlands. These findings were in direct opposition to the deep groundwater connectivity model (e.g., (Rozkowski 1967, Miller 1969, Lissey 1971, Sloan 1972, LaBaugh et al. 1987, Arndt and Richardson 1989, Richardson et al. 1992, Winter and Rosenberry 1995, LaBaugh et al. 1998). However, I also showed that intermontane depressional wetlands might be connected between wetlands through temporary surface water and longer-term soil-water pathways. These hydrologic connections may have profound effects on system hydrology and wetland ecosystem structure and function.

I organized this aspect of the research experimental design by stratifying a random sample of wetlands in the context of landscape-scale hydrogeomorphic connection or hydrogeomorphic isolation (i.e., having or not having a surface-water /soil-

water connection to an adjacent wetland) based on the appearance of indicators of connectivity. I compared selected characteristics of hydrology, surface water chemistry, and vegetation structure between isolated and connected wetlands to reveal the effects of hydrologic connectivity on wetland structure and function. Based on this rationale, this research focused on the following questions: (1) Is there evidence of surface/near-surface connectivity between depressional wetlands or are they isolated hydrogeomorphic units on the landscape? (2) If there is connectivity, does it affect wetland ecosystem structure and function?

I developed the following null hypotheses based on these two questions. H_{01} : There is no significant difference in catchment or wetland morphometry or landscape position between hydrogeomorphically isolated and connected wetlands. H_{02} : There is no significant difference in hydrologic regime between isolated and connected wetlands. H_{03} : There is no significant difference in hydrologic flux between isolated and connected wetlands. H_{04} : There is no significant difference in basic water chemical characteristics between isolated and connected wetlands. H_{05} : There is no significant difference in vegetation community structure or productivity between isolated and connected wetlands.

METHODS AND MATERIALS

Determination of Isolated and Connected Wetlands

I randomly selected 34 study wetlands, which included the 15 wetlands from Chapter II, from the approximately 90 wetlands of the South Pasture. I classified each wetland as either hydrogeomorphically connected or hydrogeomorphically isolated. This hydrogeomorphic classification was accomplished by field observations of surface connections, and by interpretation of color-infrared (CIR) aerial photographs and field

verification for soil water connections. Connected wetlands appeared to have a temporary surface water and/or a soil water connection to an adjacent, up-gradient wetland. Isolated wetlands appeared to have no surface water or soil water connection to any other wetland. Therefore, isolated wetlands received water inputs only directly to the wetland surface (i.e., precipitation or blown snow) and/or indirectly as overland flow or soil water from within their catchment, but not from another wetland. Connected wetlands received water inputs directly to the wetland surface and indirectly as overland flow or soil water from their catchment, and also via temporary surface or soil-water flow from an adjacent up-gradient wetland.

Color-infrared aerial photos (1:6000) of the South Pasture were taken in September 1997. Soil-water connections were identified by vegetation as an indicator of soil moisture. Hydrologic connections between wetlands often appeared as pink reflectance between wetlands on the CIR aerial photography. However, not all pink signatures on the CIR aerial photographs were hydrologic connections. A common exception was the presence of the exotic grass *Poa pratensis* occupying more mesic sites as a result of shade or aspect (e.g., the pink area between wetlands 5 and 6 in Fig. 3 , Chapter II). All connections were dominated by upland species, and would normally be overlooked as an inter-wetland connection. However, connections had a greater cover of mesic species, higher stem density, or greater biomass than areas outside the hydrologic influence of the connection at slightly higher elevation. Whenever surface water or soil water connections between bodies of standing water were dominated by hydrophytic-wetland vegetation, the wetlands were mapped and treated as a single wetland.

Geomorphology

I measured catchment and wetland morphology using a Leica TC600 total station. Easting, northing and elevation coordinates were surveyed (± 3 cm x, y, and ± 1 cm z) on an approximate 20 m grid across the entire South Pasture study area. Additional measurements were taken at topographic highs and lows along the grid transect which resulted in >5000 survey points across the 800m by 1600m South Pasture. Each of the 34 study wetlands was surveyed in greater detail. Wetlands were surveyed approximately every 2 m along a minimum of three transects, one along the long axis and two along the short axis. Wetland boundaries were also surveyed at approximately every 2 m. The entire survey data set was transformed to an Albers projection. The CIR photos were geo-rectified using 12 control points sited on Survey Station coordinates and verified with a Global Positioning System (GPS). Using Arc/INFO 7.2 (ESRI 1999), a 1 m interval digital elevation model (DEM) was created using a kriging algorithm to interpolate elevation across the study area and integrated with the georectified composite of the color-infrared aerial photos.

Using the DEM and 1 m contour coverage I delineated catchment boundaries for each of the 34 randomly selected study wetlands. Catchment boundaries were confirmed by field verification. I calculated a weighted slope parameter for each catchment in which slope was determined using the DEM and spatially mapped by cover class. The area of each slope cover class for each catchment was calculated using Spatial Analyst in Arc/INFO 7.2 (ESRI 1999).

I delineated wetland boundaries through field interpretation of vegetation species composition, hydrology, geomorphology, and soil characteristics. The upper wetland

boundaries were established as analogous to the upper low-prairie boundary defined by Stewart and Kantrud (1971, 1972). Wetland boundaries were digitized onto the georectified composite photograph. Catchment and wetland areas were calculated using Spatial Analyst in Arc/INFO 7.2 (ESRI 1999).

Climate

Daily precipitation (PPT) data were obtained from the Desert Research Institute-Western Regional Climate Center for Ovando, Montana (weather station 246304), located at the same elevation (1400 m) ~15 km ESE of the Bandy Experimental Ranch. Evapotranspiration (ET) was measured weekly using a Class-A evapotranspiration pan located in the South Pasture. Direct PPT inputs and ET losses for wetlands were calculated on the basis of wetland surface area.

Hydrologic regimes

I examined mean hydrographic regimes (storage/time) for all wetlands. The total survey station data was separated by each study catchment for individual wetland calculations and analyses. Stored water volume for each wetland was calculated using Surfer32 software (Golden Software 1995), which uses a 3-dimensional rectangular array of elevation values to calculate volume below any user-specified reference datum elevation. Surface water elevations were recorded weekly during ice-free conditions from April through October in 1998 and 1999 using staff gauges placed within each study wetland. I expressed weekly water storage as a percentage of annual maximum storage by wetland to normalize among wetlands for differences in wetland size.

Hydrologic flux

Hydrologic flux was defined as the balance of hydrologic inputs and outputs for a wetland over specific periods of time. I measured hydrologic flux attributed to *indirect* (i.e., catchment level) hydrologic inputs and outputs, excluding *direct* precipitation inputs and evapotranspiration outputs to wetland surfaces. Because, isolated wetlands were defined as having no hydrologic inputs from adjacent wetlands, indirect hydrologic flux is a measure of intra-catchment connectivity. Whereas, connected wetlands were defined as having a hydrologic connection to an adjacent up-gradient wetland; therefore, indirect hydrologic flux for connected wetlands is a measure of intra- *and* inter-catchment connectivity.

I calculated catchment level hydrologic flux for precipitation periods marked by summer rain events and as a single over-winter period (October 1998 through March 1999). Hydrologic flux during summer was calculated as the difference in storage between the beginning and end of each period, less the direct precipitation into the wetland plus direct evapotranspiration losses for the period. Over-winter flux was calculated as the difference in storage between the end of the 1998 growing season and spring snowmelt 1999, minus direct precipitation into the wetland. Although vapor-pressure conditions for sublimation of snow likely occur at the Bandy Ranch, I assumed over-winter losses to evapotranspiration to be minimal and these were not included in over-winter mass balance calculations.

Surface-water chemistry

Specific conductance (SpC, $\mu\text{mhos}/\text{cm}^3$) and pH of standing waters were measured in each study wetland using a multi-probe HydroLab Surveyor-3. Ion concentrations in standing waters will change seasonally as a result of dilution from additional water inputs and concentration by evaporation outputs. The amount and timing of additional water inputs and outputs will be unique to each wetland and their effect will be dependent on antecedent standing water concentrations. Therefore, SpC and pH measurements were taken in April 1999 to preclude wetland specific seasonal changes in ion concentrations. Replicate measurements were taken at water depths of ~0.5 m at three locations around the perimeter of each study wetland.

Vegetation structure and function

I delineated plant communities within each study wetland in the field using 1:1000 enlargements of the color infrared aerial photos. Each plant community was digitized onto the geo-rectified photo mosaic on the “heads-up” computer display. Surface areas of each community were calculated using Arc/INFO 7.2 (ESRI 1999). I collected vegetation data between July 22 and August 18, 1998. Absolute coverage of each species was estimated as percent aerial cover within 1.0 m x 0.5-m quadrat plots. The rectangular quadrat was used to reduce sampling bias in the very narrow (<1.0 m) concentrically banded plant communities common to depressional wetlands. Repeated, random plot samples were taken within each plant community until no new species were found.

To obtain proportional coverage (i.e., relative abundance) of each species within each wetland, I calculated the following coverage types: 1) the mean coverage of each species was calculated from plot data for each community; 2) the relative coverage of each species for each community was calculated as the mean coverage of each species divided by the total coverage of all species of the community; and 3) the proportional coverage of each species for each wetland was determined as the relative coverage of each species multiplied by the surface area of the community as a percent cover of the wetland. The sum of the proportional coverages for all species within a wetland equaled 100%. I calculated species diversity for each wetland as species richness and evenness (Pielou 1969). Richness and evenness index scores were calculated from the proportional coverage data.

I estimated net primary productivity from above-ground vegetation biomass. The South Pasture was not grazed by cattle during this study and I saw no evidence of grazing by deer, elk or insects. Biomass samples were collected in late August 1998 to ensure an accurate measure of maximum standing crop. Four 0.1 m² micro-plots were located randomly within each community of each wetland and the 1998 growth (i.e., less prior year detritus) was clipped, bagged and returned to the laboratory. Samples were dried at 60 °C for 72 h and weighed (± 0.01 g). Net primary productivity (kg/m²) was estimated for each wetland by calculating the mean biomass from the 4 samples taken from each community and then multiplying by the surface area of the community. The sum of the estimated production within each community was used to calculate total wetland productivity for each wetland.

Data analysis

I performed all data analyses using SPSS for Windows 8.0 (SPSS 1997) and PC-ORD (McCune and Mefford 1999). I considered test results to be significant at $\alpha = 0.05$; however, I present all P-values throughout this paper and base suggestion of strong trends when $\alpha \geq 0.90$. Analyses were enhanced by the balanced study design of comparing equal numbers ($n=17$) of isolated and connected wetlands, except for comparisons of surface water SpC and pH. Two-isolated wetlands stored water only for the first week of study and no surface water chemistry measurements were made. Therefore, when I compared surface water SpC and pH, sample sizes for isolated and connected wetlands were $n = 15$ and $n = 17$, respectively.

Analysis of Variance for Repeated Measures (between subject effects) was used to compare hydrographic regimes for isolated and connected wetlands. Data were arcsine transformed to meet assumptions of sphericity. Comparisons of indirect hydrologic flux for isolated and connected wetlands during precipitation periods were made using independent samples t-tests when data met assumptions of normality and homogeneity of variance, otherwise data were transformed to meet these assumptions. Mann-Whitney's non-parametric test was used when data could not be transformed to satisfy assumptions of normality and homogeneity of variance. Mean values of geomorphic, hydrologic, surface water chemistry measures, and vegetation community characteristics were compared using either independent samples t-test or Mann-Whitney's non-parametric test, as appropriate. I evaluated the relative abundance of wetland vegetation species using detrended correspondence analysis (DCA) and PC-ORD software (McCune and

Mefford 1999). The primary matrix was developed from the plant composition and coverage data. The primary matrix was composed of relative abundance data of 127 species collected across the 34 study wetlands. A secondary matrix of abiotic wetland measurements: wetland area, wetland area/catchment area ratio, duration of inundation, mean annual water storage, and surface water conductivity, was used to construct joint plots within the DCA ordination. The angle and length of the joint plot illustrates the direction and strength of the relationship between the wetland species composition of the first matrix and the abiotic wetland measures of the second matrix. The joint plot lines radiate from the centroid of the ordination scores. Only variables in the second matrix with a $r^2 > 0.2$ were plotted.

RESULTS

Determination of Isolated and Connected Wetlands

Isolated and connected wetlands were found in equal abundance in the South Pasture (Fig. 13). Of the 34 wetlands randomly selected for study, 17 were classified as isolated and 17 as connected.

Geomorphology

Figure 13 is the composite photograph and a 2-m contour elevation map of the South Pasture derived from the total station survey data and georectified with the color-infrared aerial photos. The 2-m elevation contours illustrated in Figure 13 show a north to south decline in elevation of approximately 100 m and the distribution of the study wetlands. There was no difference in elevation between isolated and connected wetlands ($T = 301$, $P = 0.918$, Table 2). However, there was a strong trend for connected wetlands

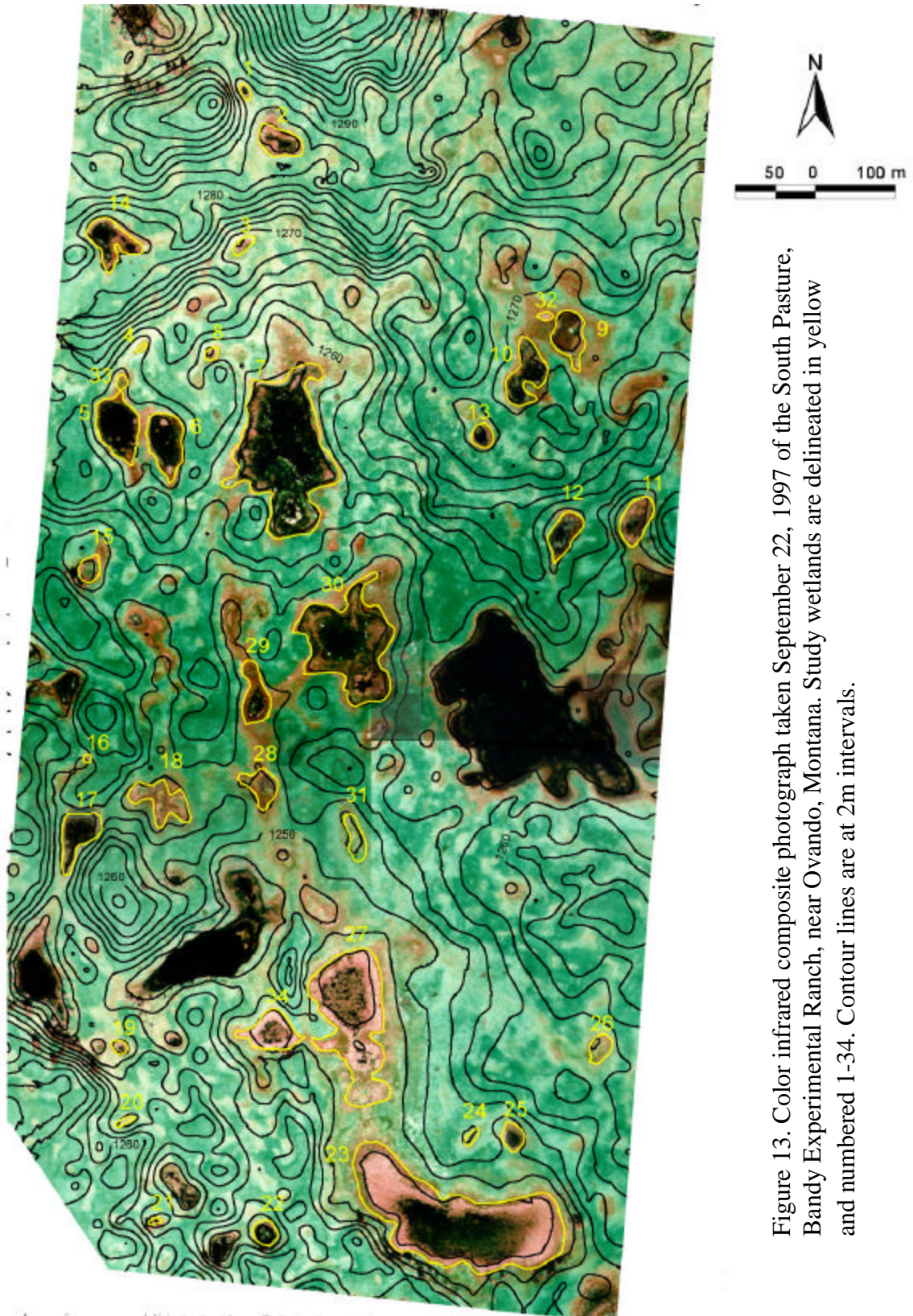


Figure 13. Color infrared composite photograph taken September 22, 1997 of the South Pasture, Bandy Experimental Ranch, near Ovando, Montana. Study wetlands are delineated in yellow and numbered 1-34. Contour lines are at 2m intervals.

Table 2. Descriptive statistics and results of comparing means of geomorphic, hydrologic, and vegetation characteristics of hydrogeomorphically isolated and connected wetlands.

		Isolated wetlands			Connected wetlands			Test statistic
Variable	Unit	Mean	1 SE	Min-Max	Mean	1 SE	Min-Max	P
Geomorphology								
Wetland area	m ²	887.9	197.7	62.8-2545.4	4188.4	1446.9	64.0-19271.9	0.073 b
Catchment area	ha	7.09	0.95	1.91-15.23	12.92	3.51	1.24-55.18	0.119 a
Wetland:catchment ratio	none	0.11	0.02	0.01-0.26	0.23	0.04	0.03-0.55	0.013 b
Catchment weighted slope	%	16.8	1.2	6.0-26.3	12.0	0.9	5.5-18.2	0.002 b
Wetland elevation	m	1256.8	2.9	1246.6-1282.8	1254.9	1.9	1244.1-1267.1	0.918 b
Hydrology								
Duration of inundation	wk/y	18.5	3.6	0-52	33.4	4.1	14-52	0.010 a
Mean annual storage	m	165.1	63.0	0-995.2	2082.2	855.4	8.11-11358.3	0.011 b
Surface water chemistry								
Specific conductivity	µmhos/cm ³	114.0	33.1	28.9-544.0	382.2	60.2	38.6-830.0	0.006 b
pH	-log(H ⁺)	7.07	0.103	6.5-8.14	7.38	0.097	6.64-8.03	0.037 a
Vegetation								
Species richness	#	31.5	2.2	18-44	37.1	3.1	14-59	0.149 a
Species evenness	none	0.66	0.01	0.57-0.77	0.60	0.02	0.40-0.72	0.008 a
Net primary productivity	g/m ²	710.5	32.5	373.6-979.8	950.5	64.9	564.9-1488.5	0.012 b

a Independent samples t-test

b Mann-Whitney nonparametric test

to be larger than isolated wetlands ($T = 245$, $P = 0.073$, Table 2). Figure 14 is the slope cover map of the South Pasture derived from the DEM and Spatial Analyst in Arc/INFO 7.2 (ESRI 1999) and illustrates the slope cover classes within study wetland catchments. Catchment weighted slope was steeper for isolated wetlands than for connected wetlands ($t = 3.285$, $df = 32$, $P = 0.002$, Table 2). There was no difference in catchment area ($t = -1.063$, $df = 32$, $P = 0.119$, Table 2) between isolated and connected wetlands, but the wetland:catchment ratio for isolated wetlands was smaller than for connected wetlands ($T = 224.5$, $P = 0.013$, Table 2). In other words, the catchment areas of connected wetlands were proportionally smaller than catchment areas of isolated wetlands.

Climate

Annual precipitation for 1998 was 41.5 cm, ~25% higher than the long-term average (33.3 cm). Annual precipitation for 1999 was 27.3 cm, ~18% below the long-term average (Fig. 4, Chapter 2).

Hydrologic regimes

Maximum water storage for all 34-study wetlands was observed in spring of both years (Fig. 15), a mean of 3.6 and 2.1 weeks after surface ice melted in 1998 and 1999, respectively. Mean water storage declined similarly throughout the summer of both years, with minimum water levels observed in the late fall (Fig. 15).

During 1998, substantial precipitation occurred during four well-defined periods in May and June that resulted in increased mean water storage across all wetlands (Fig. 15A). PPT: ET ratios for these four precipitation periods was >0.65 . However, the

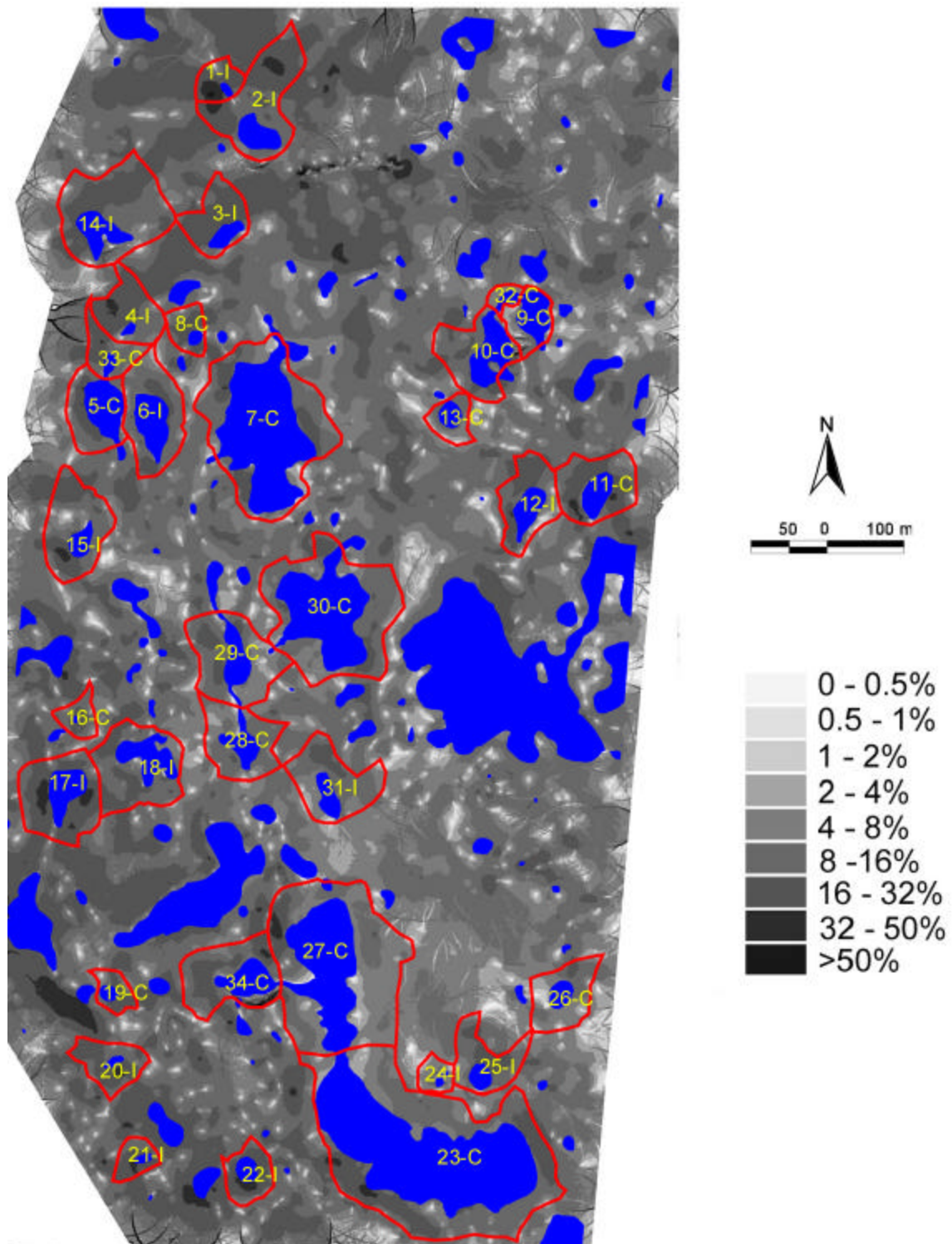


Figure 14. Geomorphic features map of the South Pasture. Grey-scale polygons refer to slope steepness classes. Red lines are catchment boundaries for study wetlands. Study wetlands are numbered 1-34. I = Isolated wetland. C = Connected wetland.

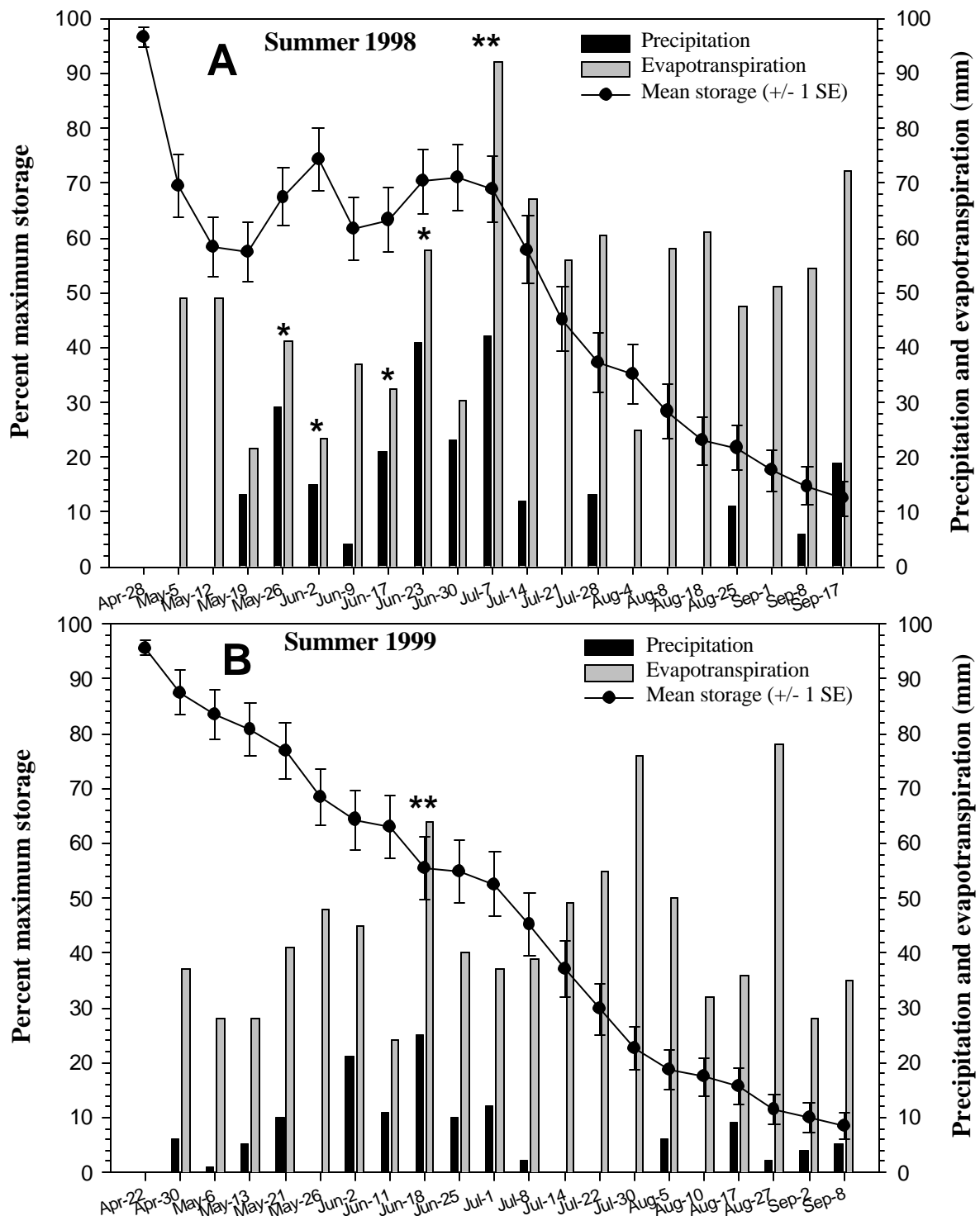


Figure 15. Mean hydrographic storage for all 34 wetlands, and weekly precipitation and evapotranspiration for the growing seasons (A) 1998, and (B) 1999. Stored water volume is expressed as percent maximum storage to normalize for size.

*notes precipitation periods that caused a mean increase in storage for all 34 wetlands.

** notes periods that received the highest precipitation each year.

precipitation period from July 1 to July 7 received the highest PPT (42 mm) in 1998, but it did not produce an increase in mean storage (Fig. 15A), nor was its PPT: ET ratio was >0.65 . In 1999, no precipitation period was observed to increase mean storage (Fig. 15B). PPT:ET ratios were <0.65 for all precipitation periods, including the period from June 12 to June 18 which had the highest precipitation (25 cm) in 1999.

Hydrographic storage patterns and storage responses to PPT and ET for isolated and connected wetlands were similar to the patterns and responses among all study wetlands (Fig. 15 and Fig. 16), yet hydrographic storage, mean annual storage, and duration of inundation between isolated and connected wetlands were significantly different. Hydrographic storage was different between isolated and connected wetlands in both 1998 (repeated measures ANOVA, $F = 8.891$, $df = 1$, $P = 0.005$, Fig. 16A) and 1999 (repeated measures ANOVA, $F = 8.007$, $df = 1$, $P = 0.008$, Fig 16B). Hydrographic storage for both isolated and connected wetlands was highest in spring, declined during periods of high evapotranspiration, and increased in response to precipitation events (Figs. 16). Connected wetlands consistently retained a higher percentage of their initial storage volume during the growing season and maintained a higher percentage of their annual maximum storage volume at the end of the year than did isolated wetlands (Fig. 16). Specifically, mean annual storage and duration of inundation were greater for connected wetlands than for isolated wetlands ($T = 223$, $P = 0.011$, $t = 3.285$, $df = 32$, $P = 0.010$, Table 2). However, isolated wetlands reached their maximum annual storage sooner than connected wetlands. Isolated wetlands reached maximum storage on average 1.6 weeks after spring snowmelt in both 1998 and 1999. In contrast, connected wetlands

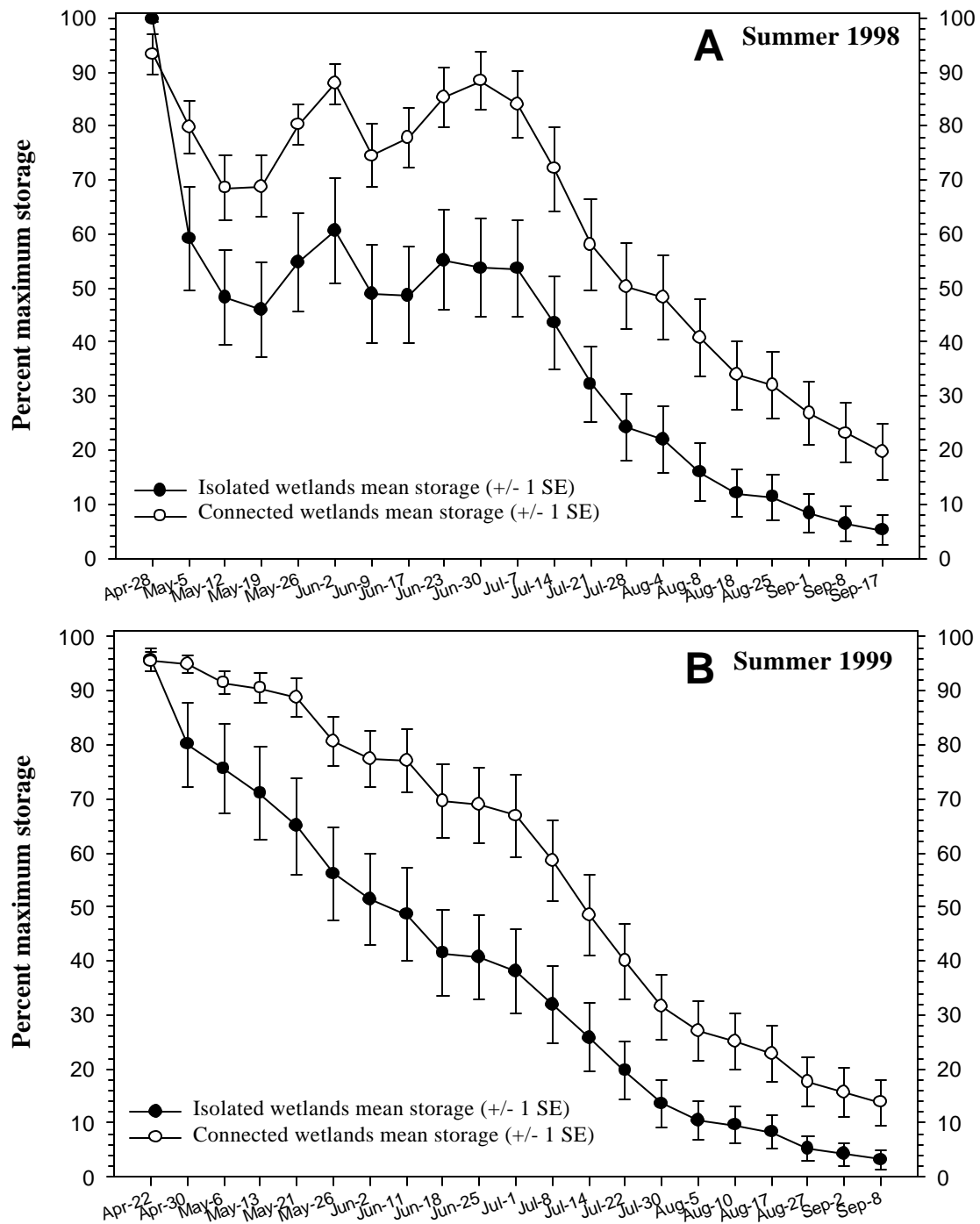
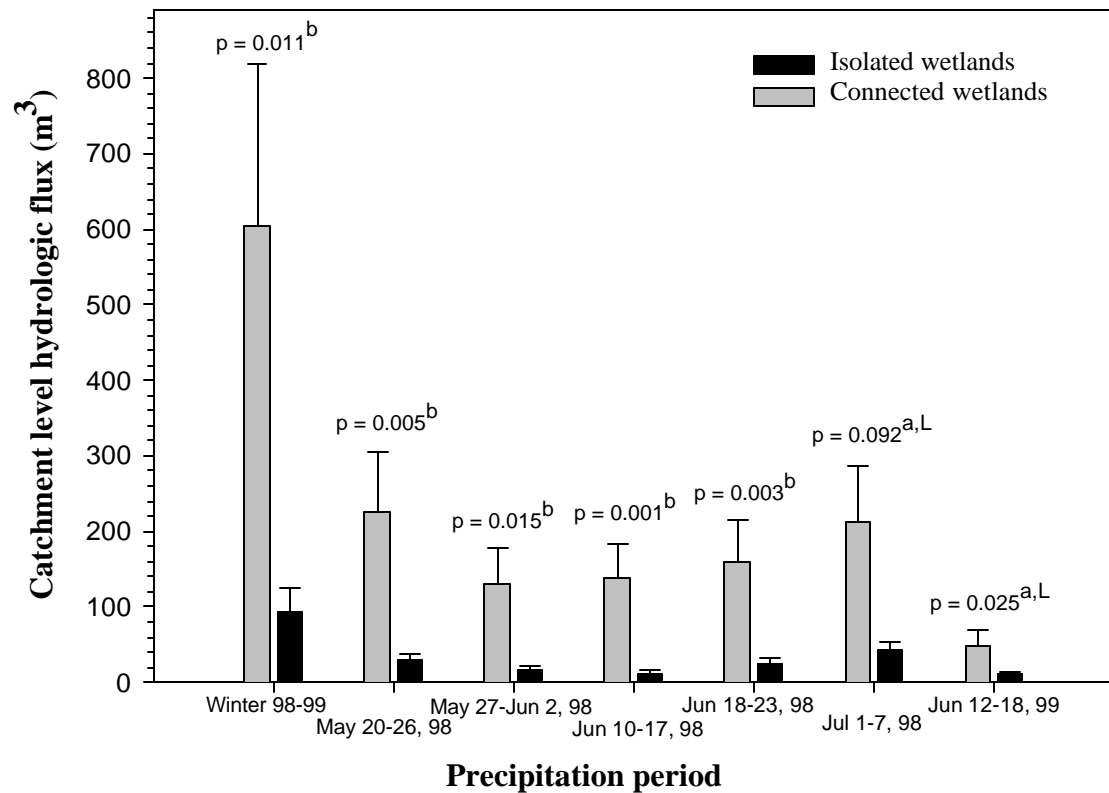


Figure 16. Mean hydrographic storage for hydrogeomorphically isolated and connected wetlands for growing seasons (A) 1998, and (B) 1999. Stored water volume is expressed as percent maximum storage to normalize for size. Repeated measures analysis of between subject effects for 1998 ($P = 0.005$) and 1999 ($P = 0.008$).

reached maximum storage in 5.6 and 2.5 weeks after snowmelt in 1998 and 1999, respectively.

Hydrologic flux

Despite connected wetlands having proportionally smaller catchments than isolated wetlands (i.e., higher wetland:catchment ratios, Table 2), connected wetlands received a greater volume of water as indirect inputs than did isolated wetlands (Fig. 17). Across all study wetlands, on average 36% of the increase in overwinter water storage came as catchment-level inputs. Connected wetlands tended to receive a higher percentage (43.7% versus 28.1%) of their overwinter increase in storage from indirect sources than did isolated wetlands ($t = -1.813$, $df = 32$, $P = 0.079$). However, overwinter hydrologic flux resulted in connected wetlands receiving 6-times more water volume ($T = 223.0$, $P = 0.011$) than did isolated wetlands (Fig. 17). During the summer of 1998 hydrologic flux was greater for connected wetlands than isolated wetlands during all precipitation periods when rain events caused increases in mean storage (May 20-26, 1998, $T = 351.0$, $P = 0.005$; May 27-June 2, 1998, $T = 340.0$, $P = 0.015$; June 10-17, 1998, $T = 362.0$, $P = 0.001$; and June 18-23, 1998, $T = 354.0$, $P = 0.003$; see Fig. 15 and Fig. 17). Only during the period of highest summer precipitation in 1998 (July 1-70) was the difference between connected and isolated wetlands not significantly different, although the same strong trend was apparent ($t = -1.743$, $df = 32$, $P = 0.092$). In 1999, no precipitation period resulted in a mean increase in storage for all wetlands (Fig. 15B). However, hydrologic flux for the period having the highest summer PPT (July 12-18)



Notes: a = independent samples t-test. b = Mann-Whitney's non-parametric test. L = data were log10 transformed to achieve homogeneous variance assumption.

Figure 17. Volumetric catchment level hydrologic flux (means ± 1 SE) for isolated and connected wetlands from overwinter and summer precipitation periods. Catchment level hydrologic flux is the net balance of catchment level hydrologic inputs and outputs.

was greater for connected wetlands than isolated wetlands ($t = -2.386$, $df = 32$, $P = 0.025$).

Surface-water chemistry

Mean specific conductance ($\mu\text{mhos}/\text{cm}^3$) of surface waters was three times higher in connected wetlands than isolated wetlands ($T = 174.0$, $P = 0.006$, Table 2). Isolated wetlands had a near neutral pH of 7.07 while connected wetlands were slightly basic with a mean pH of 7.38 (Table 2). Although this mean difference appears to be small, it was significant ($t = -2.179$, $df = 32$, $P = 0.037$).

Vegetation structure and function

Connected wetlands were more productive than isolated wetlands. Mean NPP (kg/m^2) was greater ($T = 224.0$, $P = 0.012$) among communities of connected wetlands than isolated wetlands (Table 2). Total macrophyte species richness (gamma diversity) across all wetlands was 127 species. However, the distribution of these species demonstrated strong affinities among some species for either wetland type. Forty-two species were found exclusively in either isolated or connected wetlands; 25 of these were found only in isolated wetlands and 17 only in connected wetlands. Among species only found in connected wetlands, *Scirpus acutus* (Alkali bulrush), *Crepis runcinata* (Meadow hawksbeard), and *Ranunculus cymbalaria* (Saline buttercup) had the highest frequencies of occurrence. *Grenellia howellii* (Howell's gumweed) a species considered very rare globally and very rare and imperiled in Montana (MNHP 2001) occurred only in 2 isolated wetlands.

Species evenness was significantly lower ($t = 2.828$, $df = 32$, $P = 0.008$) among connected wetlands (Table 2). However, species richness did not differ between wetland types ($t = -1.478$, $df = 32$, $P = 0.149$). Similarly, alpha diversity for isolated and connected wetlands was 102 and 110, respectively. Likewise, Shannon's diversity index (H') was not different between isolated and connected wetlands ($t = 1.585$, $df = 32$, $P = 0.123$).

The composition of wetland plant communities was highly different between isolated from connected wetlands. Detrended correspondence analysis (DCA; Fig. 18A) showed that species composition of wetlands was highly aligned with Axis 1, suggesting that wetland species composition is determined by relatively simple environmental gradients. Mean ordinal wetland scores were significantly different between isolated and connected wetlands for Axis 1 ($t = -3.285$, $df = 32$, $P = 0.002$), but not for Axis 2 ($t = -1.097$, $df = 32$, $P = 0.281$). Joint plot vectors for the environmental variables: wetland area, wetland:catchment ratio, duration of inundation, mean annual storage, and surface water specific conductance and pH were also strongly aligned with Axis 1 (Fig. 18B). This suggests strong correlation of wetland types, vegetation structure along these geomorphic, hydrologic, and water chemistry gradients.

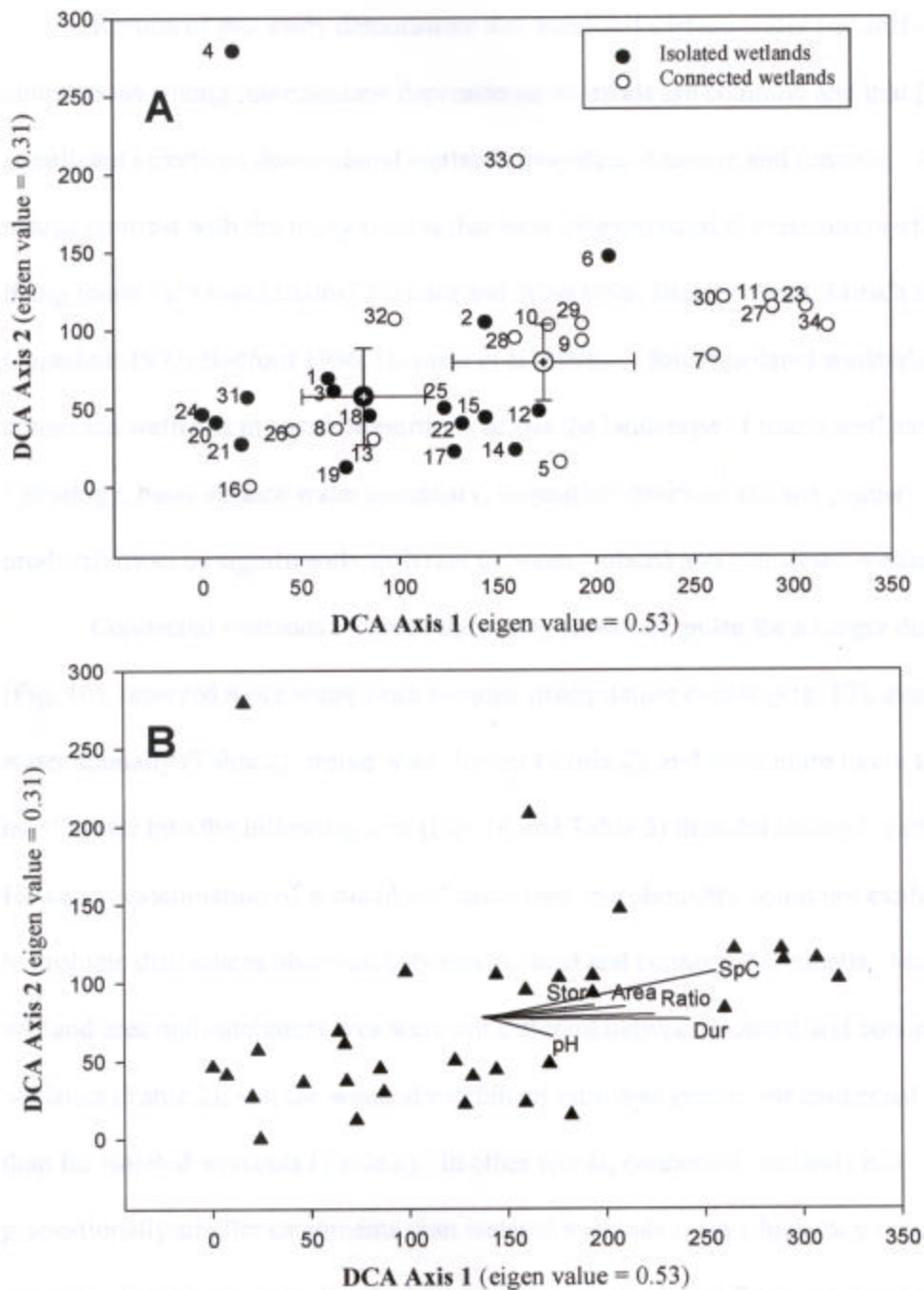


Figure 18. Detrended correspondence analysis (DCA) of hydrogeomorphologically isolated and connected wetlands using macrophyte species composition and coverage data. A) Mean ordinal wetland scores for Axes 1 and 2 are shown ± 2 SE. B) Joint plot vectors for mean annual storage, wetland area, wetland:catchment ratio, surface water specific conductivity and pH, and mean annual storage are shown.

DISCUSSION

Results of this study demonstrate that localized surface-water and soil-water connections among intermontane depressional wetlands are common and that they have significant effects on depressional wetland ecosystem structure and function. These results contrast with the many studies that have characterized depressional wetlands as being found in “closed basins” (Winter and Woo 1990, Brinson 1993, Mitsch and Gosselink 1993, Bedford 1996, Hayashi et al. 1998). I found isolated wetlands and connected wetlands in equal proportions across the landscape. I found wetland hydrology, basic surface water chemistry, vegetation structure and net primary productivity to be significantly different between isolated and connected wetlands.

Connected wetlands received the spring snowmelt pulse for a longer duration (Fig. 16), received more water from summer precipitation events (Fig. 17), stored more water annually (Table 2), stored water longer (Table 2), and were more likely to “carry-over” water into the following year (Fig. 16 and Table 2) than did isolated wetlands. However, examination of wetland and catchment morphometry could not explain the hydrologic differences observed between isolated and connected wetlands. Mean wetland area and catchment area were not different between isolated and connected wetlands (Table 2); yet, the wetland:catchment ratio was greater for connected wetlands than for isolated wetlands (Table x). In other words, connected wetlands had proportionally smaller catchments than isolated wetlands from which they received greater indirect hydrologic inputs during spring snowmelt and from summer precipitation (Fig. 17). This apparently counterintuitive result can be best explained by the temporary surface-water (during spring snowmelt) and long-term soil-water inputs (throughout the

year) that wetlands I classified as connected received from adjacent, up-gradient wetlands.

The discovery of these temporary surface-water and soil-water connections to depressional wetland hydrology has great mechanistic value and important ecological implications for our understanding the landscape distribution of dissolved solutes and the distribution, abundance, and productivity of wetland plants. Surface water SpC and pH were higher in connected wetlands than isolated wetlands. Surface water chemistry in closed basins generally experiences increased salinity (specific conductance) because solute concentrations are governed by inputs of dissolved ions from overland flow and concentration by evaporation (Hutchinson 1957, Hardie and Eugster 1970, Wetzel 1975, 1983). My comparison of hydrographic storage between isolated and connected wetlands (Fig. 16) indicated that isolated wetlands loose a greater percentage of their stored water than connected wetlands, which should lead to greater concentration of ions among the isolated wetlands. Furthermore, isolated wetlands had significantly smaller wetland:catchment ratios, which indicate that the wetland occupied a smaller portion of the catchment than did connected wetlands. This also should lead to a higher concentration of ions. However, I observed just the opposite character of dissolved solutes between these two wetland types. My results suggest that surface water chemistry for isolated wetlands are governed by the fundamental principles of ion concentration in closed basins (Hutchinson 1967, Hardie and Eugster 1970, Wetzel 1975, 1983). In contrast, connected wetlands can potentially gain and loose water via temporary surface and near-surface inputs and outputs. The net effects of connectivity were (1) greater inputs than outputs (i.e., positive hydrologic flux for all precipitation periods; Fig. 17)

and (2) a higher likelihood of “carry-over” stored water into the following spring. Long-term repetition of these inputs by connected wetlands provides a mechanism for higher dissolved ion concentrations in surface waters when comparing connected wetlands to isolated wetlands. In other words, surface water chemistry is strongly related to connectivity.

Surface and soil-water connectivity, as a mechanism for determining basic surface-water chemistry, offers an alternative explanation to the deep groundwater connection paradigm that models wetland salinity (specific conductivity) to be inversely related to wetland elevation (Sloan 1972, LaBaugh et al. 1987, Arndt and Richardson 1988, 1989, Richardson et al. 1992). Similarly to Swanson et al. (1988) I found no relationship between wetland elevation and wetland water chemistry. I also found no relationship between wetland elevation and wetland connectivity or isolation. Rather, I found that connected wetlands had higher specific conductivity and pH than isolated wetlands (Table 2).

The physiological constraints on wetland plants associated with salinity and inundation are a likely explanation for the changes in species composition observed among the wetlands of this study. Similar relationships have been hypothesized for depressional prairie pothole wetlands of central North America (Stewart and Kantrud 1971 and 1972, Kantrud et al. 1989). The results of my study suggest that differences in wetland water chemistry and hydrology were associated with substantial differences in wetland vegetation structure. Macrophyte species composition, net primary productivity, and species evenness were all significantly different between isolated and connected wetlands, and strongly affected by environmental gradients (Fig. 18A).

Surface water specific conductance and duration of inundation were highly correlated with species composition (Fig. 18B). Mean ordinal scores of the Detrended Correspondence Analysis revealed that isolated and connected wetlands were significantly different along Axis 1 and that the differentiation of wetland vegetation corresponded to these environmental gradients. Due to the physiological constraints associated with osmoregulation in fresh water, macrophytes (Hutchinson 1967, Wetzel 1975, 1983) and nonhalophytes (Greenway and Munns 1980) have developed various mechanisms to accommodate both low oxygen concentrations in the root zone caused by inundation and high concentrations of salts (see Mitsch and Gosselink 1993).

Net primary productivity of wetland macrophytes was significantly greater among connected wetlands compared to isolated wetlands (Table 2). This may be a reflection of greater nutrient availability and/or greater water availability. Nutrients in solution or in sediment are likely carried to wetlands by surface waters as overland flow or via inter-catchment connections through the soil-water. Whether the significant difference in productivity is a result of greater nutrient or water availability, both are strongly associated with differences in water chemistry and hydrology as results of landscape-level processes and inter-catchment connectivity.

The observed differences in vegetation structure and function may be explained by the differences in hydrologic complexity and stability (*sensu* MacArthur 1958, MacArthur and MacArthur 1961 and Tilman 1977, 1988). As I hypothesized above, differences in annual precipitation patterns could create greater inter-annual variation of storage among connected wetlands than isolated wetlands. Thus, greater species

evenness among isolated wetlands (Table 2) may be a reflection of a less complex hydrologic environment.

In conclusion, many researchers have identified surface water inputs and evapotranspiration outputs as the major components of the hydrologic budget for depressional wetlands (Shjeflo 1968, Eisenlohr et al. 1972, Sloan 1972, Winter and Rosenberry 1995, Parkhurst et al. 1998, LaBaugh et al. 1998), yet few studies suggest that landscape-level geomorphology and surface hydrology can strongly influence depressional wetland hydrology (Euliss and Mushet 1996). This study provides an emerging picture of depressional wetland ecology that establishes the subtle “natural corridors” of surface and near-surface hydrologic exchange among wetlands as primary mechanisms mediating depressional wetland structure and function (Fig. 19). Subtle topographic low points between wetlands establish near-surface soil-water connections among some wetlands, while others remain isolated on the landscape. I have shown that these subtle, often-ignored, temporary surface and near-surface hydrologic connections between previously considered “closed-basins” have significant effects on the hydrographic storage of intermontane depressional wetlands in both wet and dry years. Hydrologic connectivity had strong correlations to surface water chemistry, macrophyte species composition, diversity, and net primary productivity. My results provide strong evidence that depressional wetland hydrology, water chemistry, and vegetation structure are inextricably tied to landscape-level processes, which in turn play a controlling role in the ecological variation seen among intermontane depressional wetlands. It is also reasonable to assume that surface water chemistry and vegetation structure, as primary response characteristics, will also affect food webs and higher trophic interactions. These

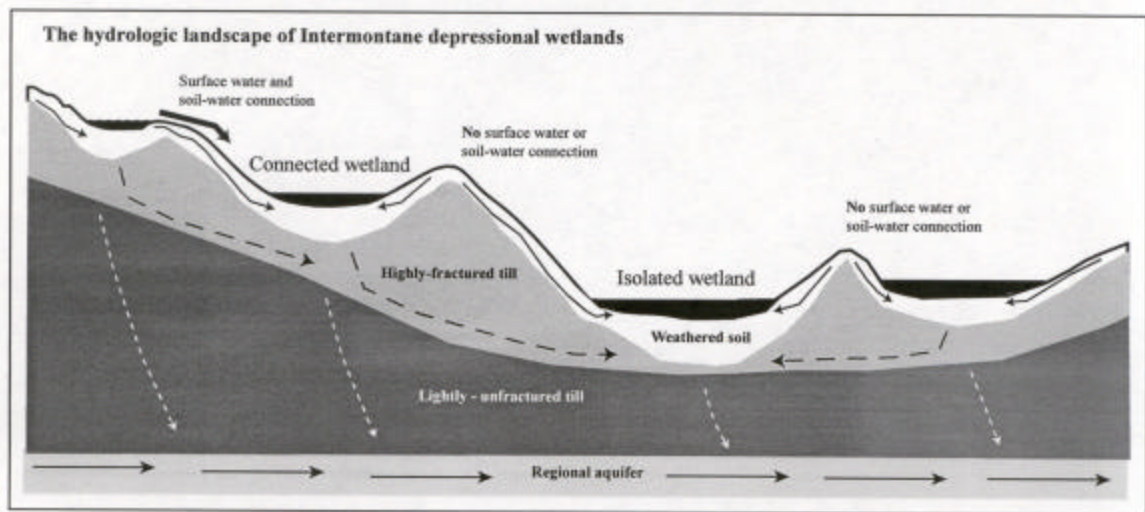


Figure 19. Generalized diagram illustrating the hydrologic landscape of inter-montane depressional wetlands. Spatial variation in topography and soil development/till fracturing affects spatial and temporal surface-water and soil-water connections between wetlands, creating a hydrogeomorphic template where isolated and connected wetlands can be found at any elevation in the landscape.

results have implications for ecologists, conservationist, and managers alike. Clearly, whether in regard to either future research or management of these systems, it can no longer be an accepted view that depressional wetlands are isolated ecosystems on the landscape.

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APPENDIX ONE

Correlation analyses between geomorphic, hydrologic, water chemistry, and vegetation structure of (A) hydrogeomorphologically isolated and (B) hydrogeomorphically connected wetlands.

A) Hydrogeomorphically isolated wetlands

	Geomorphology				Hydrology		Surface water chemistry		Vegetation structure		
	Wetland: catchment ratio	Catchment area (m ²)	Catchment weighted slope (%)	Wetland elevation (m)	Duration of inundation (wk/y)	Mean annual storage (m ³)	Specific conductivity (µmhos/cm ³)	pH	Species richness	Species evenness	Net primary productivity (g/m ²)
Wetland area (m ²)	0.87 (<0.0000)	0.81 (<0.0000)	-0.19 (0.4715)	0.71 (0.786)	0.73 (0.0010)	0.79 (0.0002)	0.60 (0.0173)	0.73 (0.0019)	0.69 (0.0023)	-0.29 (0.2552)	0.03 (0.9136)
Wetland: catchment ratio		0.47 (0.0588)	-0.28 (0.2835)	-0.143 (0.585)	0.80 (0.0001)	0.80 (0.0001)	0.60 (0.0178)	0.76 (0.0011)	0.79 (0.0002)	-0.33 (0.2004)	-0.24 (0.3458)
Catchment area (m ²)			-0.10 (0.7004)	0.25 (0.325)	0.39 (0.1210)	0.46 (0.0629)	0.37 (0.1782)	0.50 (0.0552)	0.46 (0.0618)	-0.10 (0.6970)	0.32 (0.2091)
Catchment weighted slope (%)				0.47 (0.058)	0.01 (0.9804)	-0.12 (0.6421)	-0.15 (0.5980)	-0.28 (0.3136)	-0.10 (0.6979)	0.16 (0.5412)	0.40 (0.1072)
Wetland elevation (m)					-0.080 (0.763)	-0.05 (0.852)	0.15 (0.604)	-0.261 (0.348)	-0.06 (0.832)	0.22 (0.403)	0.26 (0.318)
Duration of inundation (wk/y)						0.91 (<0.0000)	0.64 (0.0096)	0.65 (0.0084)	0.71 (0.0013)	-0.35 (0.1657)	-0.08 (0.7485)
Mean annual storage (m ³)							0.83 (0.0001)	0.77 (0.0007)	0.60 (0.0106)	-0.46 (0.0616)	0.04 (0.8653)
Specific conductivity (µmhos/cm ³)								0.73 (0.0022)	0.44 (0.1044)	-0.42 (0.1168)	0.21 (0.4509)
pH									0.56 (0.0313)	-0.45 (0.0888)	0.02 (0.9307)
Species richness										-0.10 (0.7016)	-0.09 (0.7323)
Species evenness											-0.08 (0.7608)

Values given are Pearson correlation coefficients (*r*) with probability values (*P*) in parentheses. Values in bold are significant at *P* = 0.05 after sequential Bonferroni corrections (*α* = 0.05/66).

B) Hydrogeomorphically connected wetlands

	Geomorphology				Hydrology		Surface water chemistry		Vegetation structure		
	Wetland: catchment ratio	Catchment area (m ²)	Catchment weighted slope (%)	Wetland elevation (m)	Duration of inundation (wk/y)	Mean annual storage (m ³)	Specific conductivity (µmhos/cm ³)	pH	Species richness	Species evenness	Net primary productivity (g/m ²)
Wetland area (m ²)	0.69 (0.0021)	0.96 (<0.0000)	-0.04 (0.8809)	-0.46 (0.066)	0.67 (0.0035)	0.98 (<0.0000)	0.49 (0.0449)	0.18 (0.4862)	0.44 (0.0792)	-0.36 (0.1609)	0.52 (0.0340)
Wetland: catchment ratio		0.55 (0.0234)	-0.09 (0.7355)	-0.03 (0.908)	0.64 (0.0057)	0.67 (0.0036)	0.40 (0.1162)	0.37 (0.1380)	0.61 (0.0092)	-0.42 (0.0968)	0.14 (0.5851)
Catchment area (m ²)			-0.04 (0.8890)	-0.59 (0.013)	0.68 (0.0029)	0.92 (<0.0000)	0.58 (0.0147)	0.23 (0.3673)	0.33 (0.1951)	-0.44 (0.0761)	0.55 (0.0232)
Catchment weighted slope (%)				-0.25 (0.344)	0.06 (0.8305)	-0.02 (0.9494)	-0.01 (0.9603)	0.03 (0.9124)	0.18 (0.4968)	-0.32 (0.2031)	0.20 (0.4385)
Wetland elevation (m)					-0.65 (0.005)	-0.43 (0.087)	-0.52 (0.022)	-0.41 (0.098)	0.05 (0.859)	0.50 (0.041)	-0.42 (0.098)
Duration of inundation (wk/y)						0.63 (0.0065)	0.70 (0.0017)	0.68 (0.0029)	0.44 (0.0744)	-0.71 (0.0013)	0.16 (0.5305)
Mean annual storage (m ³)							0.42 (0.0972)	0.13 (0.6312)	0.43 (0.0828)	-0.30 (0.2419)	0.52 (0.0343)
Specific conductivity (µmhos/cm ³)								0.63 (0.0067)	0.37 (0.1410)	-0.64 (0.0053)	0.33 (0.1955)
pH									0.48 (0.0533)	-0.44 (0.0736)	-0.14 (0.5977)
Species richness										-0.25 (0.3261)	0.14 (0.5834)
Species Evenness											-0.11 (0.6766)

Values given are Pearson correlation coefficients (*r*) with probability values (*P*) in parentheses. Values in bold are significant at *P* = 0.05 after sequential Bonferroni corrections (*α* = 0.05/66).